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PROTOPANDERODUS (CONODONTATA) FROM THE ORDOVICIAN ROAD RIVER GROUP NORTHERN YUKON TERRITORY AND THE EVOLUTION OF THE GENUS

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for description

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PREFACE

Investigations of conodonts and other fossils from well exposed lower Paleozoic strata in the Cordillera of northern Yukon and western District of Mackenzie provide important information on the depositional and tectonic history of western Canada.

This report presents the systematic description of seven species of the Ordovician conodont genus *Protopanderodus* from carbonate beds within the predominantly fine grained clastic rocks of the Road River Group. In addition, the spatial and temporal distribution of *Protopanderodus* has been compiled to facilitate the interpretation of the paleoecology and evolution of this genus and its phylogenetic relationship with *Drepanodus*.

The accurate identification and description of fossils are prerequisites not only for paleobiological studies, but also for biostratigraphy, which in turn provides the essential framework for the exploration of mineral and energy resources in Canadian sedimentary basins.

Elkanah A. Babcock
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PRÉFACE

Les études sur les conodontes et les autres fossiles trouvés dans les couches géologiques bien exposées du Paléozoïque inférieur dans la Cordillère du nord du Yukon et de l'ouest du district de Mackenzie fournissent d'importants renseignements sur l'histoire sédimentaire et tectonique de l'Ouest canadien.

Le présent rapport fait la description systématique de sept espèces de conodontes du genre *Protopanderodus* de l'Ordovicien qui ont été extraites de lits carbonatés compris dans les roches clastiques à grain fin prédominant du groupe de Road River. En outre, la répartition spatio-temporelle de *Protopanderodus* a été compilée de manière à faciliter l'interprétation de la paléoécologie et de l'évolution de ce genre et de sa parenté phylogénétique avec *Drepanodus*.

L'identification et la description précises des fossiles sont des préalables, non seulement aux études paléobiologiques, mais aussi à la biostratigraphie, laquelle fournit à son tour le cadre essentiel à la prospection des ressources minières et énergétiques dans les bassins sédimentaires du Canada.

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PROTOPANDERODUS (CONODONTATA) FROM THE ORDOVICIAN ROAD RIVER GROUP, NORTHERN YUKON TERRITORY, AND THE EVOLUTION OF THE GENUS

Abstract

Ordovician conodont faunas from four sections of the Road River Group in the Blackstone and Richardson troughs of northern Yukon Territory contain a total of seven species of *Protopanderodus* (*P. insculptus*, *P. liripipus*, *P. parvibasis*, *P. robustus*, *P.* cf. *P. varicostatus*, *P.* n. sp. A, and *P.* sp. B). The 115 elements of *Protopanderodus* represent about 12 per cent of the total collection. The conodonts are from carbonate beds within fine grained clastic and graptolitic strata and range in age from at least early Llanvirn to late Ashgill. Distribution of *Protopanderodus* in the northern Canadian Cordillera, and elsewhere, shows that it was common in offshore environments, whereas it is rare (0-4 relative per cent) in strata of the more nearshore carbonate facies of southwestern Northwest Territories.

Protopanderodus and *Drepanodus* are related at the family level. *Protopanderodus* is characterized by a costae- and torsion-symmetry transition series of acontiodontiform (*a/b-c*) elements, which exhibit variable curvature, and scandodontiform (*e*) elements. Elements of *Drepanodus* form a cusp-curvature and torsion-symmetry transition series (*a/b-c*), and scandodontiform (*e*) elements.

The precursor of *Protopanderodus*, thought to be similar to *P.* n. sp. A, had probably evolved from *Drepanodus* by the early Arenig. Species of *Protopanderodus* are assigned to two morphological groups that represent phylogenetic lineages. The bicostate group comprises *a/b-c* elements with two or less costae, and smooth to weakly grooved *e* elements. Species of the multicostate group have *a/b-c* elements with two or more costae and *e* elements that are noticeably grooved. Both groups existed by the middle Arenig; the bicostate lineage terminated in the Caradoc, and the multicostate lineage continued to the late Ashgill. Some major events in the evolution of *Protopanderodus* coincided with eustatic events.

Résumé

Des faunes de conodontes de l'Ordovicien provenant de quatre coupes du groupe de Road River dans les fosses de Blackstone et de Richardson, dans le nord du Yukon, contiennent au total sept espèces de *Protopanderodus* (*P. insculptus*, *P. liripipus*, *P. parvibasis*, *P. robustus*, *P.* cf. *P. varicostatus*, *P.* n. sp. A et *P.* sp. B). Les 115 éléments de *Protopanderodus* représentent 12 % environ toute de la collection. Les conodontes proviennent de couches carbonatées intercalées dans des couches de roches clastiques à grain fin et renfermant des graptolites; leur âge varie du Llanvirnien inférieur, au moins, de l'Ashgillien supérieur. La répartition de *Protopanderodus* dans le nord de la Cordillère canadienne et ailleurs témoigne de l'abondance relative de cette espèce au large des côtes; d'autre part sa présence se fait rare (de 0 à 4 % relatif) dans les couches du faciès carbonaté le plus littoral du sud-ouest des Territoires du Nord-Ouest.

Il existe un lien au niveau de la famille entre *Protopanderodus* et *Drepanodus*. Chez *Protopanderodus*, les éléments acontiodontiformes (*a/b-c*), que caractérise leur courbure variable, et les éléments scandodontiformes (*e*) correspondent à une série transitionnelle quant à la symétrie des côtes et à la symétrie de torsion. Les éléments de *Drepanodus* constituent une série de transition quant à la courbure des cuspides et à la symétrie de torsion (*a/b-c*), de même que des éléments scandodontiformes (*e*).

Le précurseur de *Protopanderodus*, que l'on croyait semblable à *P.* n. sp. A, s'est probablement différencié de *Drepanodus* avant l'Arénigien inférieur. Les espèces de *Protopanderodus* ont été réparties dans deux groupes morphologiques qui représentent des lignées phylogénétiques. Le groupe à deux côtes comprend les éléments *a/b-c* avec au moins deux côtes ainsi que les éléments *e* lisses ou faiblement rainurés. Les espèces du groupe à plusieurs côtes comprennent les éléments *a/b-c* avec deux côtes ou plus ainsi que les éléments *e* qui sont nettement rainurés. Les deux groupes ont existé avant l'Arénigien moyen; la lignée à deux côtes s'est terminée au cours du Caradocien et la lignée à plusieurs côtes s'est poursuivie jusqu'à de l'Ashgillien supérieur. Certaines étapes importantes de l'évolution de *Protopanderodus* ont coincidé avec des événements eustatiques.

Summary

Ordovician conodont collections from four sections of the Road River Group in northern Yukon (Fig. 1) have yielded relatively few elements of *Protopanderodus* (Table 1). They do however, contain five known species of *Protopanderodus* and two unnamed species [*P. insculptus* (Branson and Mehl), *P. liripipus* Kennedy et al., *P. parvibasis* Löfgren, *P. robustus* (Hadding), *P.* cf. *P. varicostatus* (Sweet and Bergström), *P.* n. sp. A, *P.* sp. B]. Elements of *P.* n. sp. A are similar to elements previously assigned to *Drepanodus*; their assignment to *Protopanderodus* rather than *Drepanodus* was aided by the discovery of a fused cluster.

The conodonts are from rare limestone beds within sequences of graptolite-rich shale, calcareous shale, and chert, all of which represent the basinal, fine grained clastic facies of the Blackstone Trough, which trends west-southwest and the nearby Richardson Trough, which trends north-northwest. Both troughs were bordered by platform-margin carbonate environments during the Ordovician and Silurian.

The biostratigraphic occurrences of the *Protopanderodus* faunas in northern Yukon are as follows. Those from the Blackstone River are within the *Gamachignathus ensifer* Conodont Zone, and occur 13.7 m above graptolites of the *Paraorthograptus pacificus* Zone and 3 m below graptolites tentatively assigned to the *Glyptograptus persculptus* Zone. This conodont fauna represents the upper Richmondian and upper Ashgill.

Two faunas are identified from the section at Peel River. The lower is within the *Pygodus serra* Conodont Zone, and occurs between beds indicative of the *Paraglossograptus tentaculatus* (3.9 m below) and *Diplograptus decoratus* (18.3 m above) zones. The stratigraphic level of this conodont fauna is regarded as middle Llanvirn. The higher conodont fauna is indicative of the *Gamachignathus ensifer* Zone and is within the upper Ashgill *Paraorthograptus pacificus* Zone. The sample level is only 1.9 m below the lower Llandovery *Parakidograptus acuminatus* Zone.

Associated with glossograptids, and 56 m below a rather undiagnostic collection of Llandeilo – Caradoc graptolites from Rock River, there is a conodont fauna that contains species of *Protopanderodus*. This fauna is probably upper Arenig or lower Llanvirn. Higher in the Rock River section are two sparse, presumably Caradoc – Ashgill, conodont faunas. Graptolites in strata contiguous to this upper faunal level represent the *Dicellograptus ornatus* to *Paraorthograptus pacificus* zones.

Protopanderodus at the Tetlit Creek section is from a conodont fauna that has a range of lower Llanvirn to upper Llandeilo. The graptolites 38 m below this level are rather undiagnostic Arenig – Llanvirn forms, those 36 m above indicate the upper Llandeilo – lower Caradoc *Nemagraptus gracilis* Zone.

The distribution of *Protopanderodus* from middle Arenig to Ashgill, in the fine grained clastic facies of northern Yukon and southwestern Northwest Territories, and in the carbonate facies of the latter area, confirms the known distribution of the genus. Species of *Protopanderodus* were more common in the offshore environments, which in this part of Laurentia are represented by the clastic-rich Road River Group. For example, only 0.2 percent of the more than 9000 elements in the Richmondian collections from the marginal carbonate platform of the Whittaker Formation in southwestern Northwest Territories are of *Protopanderodus* (Nowlan et al., 1988). In equivalent strata of the Road River Group at Blackstone and Peel rivers in northern Yukon, conodont faunas contain 13 percent *Protopanderodus*. Similar examples can be given for older strata. In the Arenig – Llanvirn, *Protopanderodus* represents about 11 to 56 percent of the fauna in strata of the Road River Group, whereas it is rare or absent in the equivalent carbonate facies.

Protopanderodus had probably evolved from *Drepanodus* by the early Arenig. Evolution may have been from a species of *Drepanodus* with an apparatus of elements that constitute primarily a cusp-curvature transition series, with a less obvious symmetry transition character – displayed by the torsion of the elements (torsion-symmetry) and rarely costate ornamentation (costae-symmetry) – to a species of *Protopanderodus* in which the costae-symmetry transition is more apparent. In early species of *Protopanderodus*, this symmetry is shown by the position of ornamentation on uni- and bicostate elements, and by the torsion of the elements; elements of *Protopanderodus* also exhibit variable curvature.

The difference between the apparent symmetry of *Drepanodus* and *Protopanderodus* is further exaggerated by the multiple and highly sculptured nature of ornamentation in younger species of *Protopanderodus*. Even in these multicostate species, variable torsion and curvature are still present.

Both *Drepanodus* and *Protopanderodus* are assigned herein to the Family Protopanderodontidae; the former being in the Subfamily Drepanodontinae, and the latter in the Subfamily Protopanderodontinae.

The Drepanodontinae are characterized by a cusp-curvature transition series of variably twisted acostate to rarely costate *a/b-c* (drepanodontiform) and acostate *e* (scandodontiform) elements, and consist of *Drepanodus* and *Parapaltodus*. The Protopanderodontinae, represented only by *Protopanderodus*, comprise variably twisted (torsion-symmetry) unicostate to multicostate *a/b-c* (acontiodontiform) elements within a costae-symmetry and cusp-curvature transition series, and acostate, carinate or costate *e* (scandodontiform) elements. These subfamilies are distinct from the Subfamily Drepanoistodinae of the Family Drepanoistodontidae. The Drepanoistodinae are represented by the genera *Drepanoistodus*, *Paltodus*, *Paroistodus*, and possibly *Besselodus*, and are characterized by a cusp-curvature transition series of variably twisted *a/b-c* (one to two distinct drepanodontiform) elements, and a geniculate *e* (oistodontiform) element – all of which can vary from acostate to costate.

The *a/b-c* elements of *Protopanderodus* can at least be partially differentiated in some species. The *a/b* and *c* elements, in the simplest sense are, respectively, asymmetrical and symmetrical *a/b-c* elements. The development of posterior denticulated *a/b-c* elements, which are found in both symmetrical and asymmetrical varieties, is known only in *P. insculptus*, and represents a significant departure from the more typical apparatus.

Two phylogenetic lineages are recognized in *Protopanderodus* and are based on the degree of ornamentation (Fig. 2). The bicostate group or lineage has *a/b-c* elements with two, or less, lateral costae. This group includes species that are morphologically "transitional" between *Drepanodus* and *Protopanderodus*. Species of the bicostate lineage are: *P. elongatus* Serpagli, *P. graeai* (Hamar), *P. leonardii* Serpagli, *P. parvibasis*, *P. rectus* (Lindström), *P. robustus*, *P.* sp. Löfgren, and from northern Yukon, *P.* n. sp. A. The *e* elements of species of this lineage are variable – unicostate (*P. graeai*), smooth (*P. elongatus*, *P. robustus*, *P.* n. sp. A), carinate (*P. rectus*), or weakly carinate and grooved (*P. parvibasis*). The multicostate lineage is represented by species with *a/b-c* elements that have two or more costae. These species are: *P. insculptus*, *P. gradatus* Serpagli, *P.*? *lee* Repetski, *P. liripipus*, *P. strigatus* Barnes and Poplawski, *P. varicostatus*, *P.* sp. Dzik, and from northern Yukon, *P.* sp. B. Almost all of these multicostate species have *e* elements that are noticeably grooved on the inner face.

The principal evolutionary changes in the Protopanderodontidae are: the increase in ratio of costate to acostate elements from a species such as *Drepanodus arcuatus* Pander (which differs from *P.* n. sp. A in the proportion of acostate to costate elements) to an early species of *Protopanderodus*; the extension of costae toward the posterior aboral margin in later species of *Protopanderodus*; and the development of the two lineages.

The biocostate species *Protopanderodus elongatus* and *P. leonardii* are the oldest forms of the genus. Both occur in the lower Arenig in Texas (Repetski, 1982), and the former may be as old as late Tremadoc. The younger *P. rectus* may be the direct ancestor of *P. graeai*, *P. parvibasis*, and *P. robustus*. *Protopanderodus gradatus* may be the link between bicostate and multicostate groups. Its *c* element is bicostate, as are those of the former lineage, but its *a/b* and *e* elements are similar to elements of the latter lineage. The lower stratigraphic range of *P. gradatus* and the bicostate *P. rectus* are concurrent. The multicostate species *P.* sp. Dzik, *P. varicostatus*, *P. liripipus* and *P. insculptus* form a slightly less complex divergent lineage than the bicostate lineage.

Six notable events in the evolution of *Protopanderodus*, some of which can be linked, at least temporally, to eustatic and other faunal events, are briefly discussed below.

Attempts to relate Events 1 (transition from *Drepanodus* to an ancestral bicostate species of *Protopanderodus* by or before the early Arenig) and 2 (origin of the multicostate lineage by the middle Arenig) to eustatic changes in sea level are hampered by the lack of precision in determining the level of first appearance of species of both lineages. The appearance of the bicostate species *P. elongatus* may have been coincident with the middle Arenig trangression. However, *P. elongatus* sensu Repetski (1982) may in fact be older, and, if so, it was present during the last phase of the late Tremadoc transgression. The oldest multicostate species are *P. gradatus* sensu Serpagli (1974) and *P. varicostatus* of Gastil and Miller (1981) – both correspond to the middle Arenig transgression.

Several species of *Protopanderodus* are known from Argentina, Texas, Utah, and New Mexico. These possibly represent a Pacific fauna that included two lower Arenig bicostate species and, later, two multicostate species in the middle Arenig. The appearance of these forms predates appearances of *Protopanderodus* species in Baltica and Iapetus and suggests that the bicostate and multicostate lineages developed in the western Iapetus Ocean, or the Pacific Ocean (Event 3).

Divergence within both lineages (Event 4), coincided with a late Arenig regressive maxiumum and early Llanvirn transgression. The bicostate lineage was terminated (Event 5) in the early Caradoc during an extensive transgressive phase. Event 6, the evolution of *P. insculptus* from *P. liripipus* in the late Caradoc or early Ashgill, is the final event before the demise of both species by Late Ordovician time.

Sommaire

Les collections de conodontes de l'Ordovicien provenant de quatre coupes du groupe de Road River dans le nord du Yukon (Fig. 1) ont contribué relativement peu d'éléments de *Protopanderodus* (tab. 1). Elles contiennent cependant cinq espèces connues de *Protopanderodus* et deux espèces non désignées [*P. insculptus* (Branson et Mehl), *P. liripipus* Kennedy et coll., *P. parvibasis* Löfgren, *P. robustus* (Hadding), *P.* cf. *P. varicostatus* (Sweet et Bergström), *P.* n. sp. A, *P.* sp. B]. Les éléments de *P.* n. sp. A sont semblables aux éléments antérieurement attribués à *Drepanodus*; cette attribution à *Protopanderodus* plutôt qu'à *Drepanodus* se base sur la découverte d'un groupe fusionné.

Les conodontes proviennent de rares couches calcaires contenues dans des séquences de schiste argileux riche en graptolites, de schiste argileux calcaire et de chert qui correspondent au faciès de bassin de roches clastiques à grain fin de la fosse de Blackstone, de direction nord-nord-est, et de la fosse de Richardson voisine, de direction ouest-sud-ouest. Les deux fosses sont bordées de roches carbonatées de bordure de plate-forme mises en place au cours de l'Ordovicien et du Silurien.

Dans le nord du Yukon, la biostratigraphie des faunes de *Protopanderodus* se présente de la façon suivante : celles de la rivière Blackstone se trouvent dans la zone à conodontes *Gamachignathus ensifer*, à 13,7 m au-dessus des graptolites de la zone à *Paraorthograptus pacificus*, et à 3 m sous les graptolites qui ont été temporairement attribués à la zone à *Glyptograptus persculptus*. Cette faune de conodontes correspond au Richmondien supérieur et à l'Ashgillien supérieur.

Deux faunes ont été identifiées dans la coupe se trouvant à la rivière Peel. La faune inférieure se trouve dans la zone à *Pygodus serra* et se manifeste entre deux couches indicatrices des zones à *Paraglossograptus tentaculatus* (3,9 m au-dessous) et à *Diplograptus decoratus* (18,3 m au-dessus). Le niveau stratigraphique de cette faune de conodontes daterait du Llanvirnien moyen. La faune de conodontes supérieure est indicatrice de la zone à *Gamachignathus ensifer* et se trouve dans la zone à *Paraorthograptus pacificus* de l'Ashgillien supérieur. Le niveau d'échantillonnage ne se situe qu'à 1,9 m au-dessous de la zone à *Parakidograptus acuminatus* du Llandovérien inférieur.

Associés aux glossograptides et à 56 m sous une collection plutôt non caractéristique de graptolites llandeiliens-caradociens de la rivière Rock, se trouve une faune de conodontes qui renferme des espèces de *Protopanderodus*. Cette faune date probablement de l'Arénigien supérieur ou du Llanvirnien inférieur. Plus haut dans la coupe de la rivière Rock se trouve deux faunes de conodontes éparses datant probablement du Caradocien-Ashgillien. Les graptolites contenus dans des couches contiguës à ce niveau faunique supérieur correspondent aux zones allant de *Dicellograptus ornatus* à *Paraorthograptus pacificus*.

Protopanderodus dans la coupe du ruisseau Tetlit fait partie d'une faune de conodontes dont l'âge varie du Llanvirnien inférieur au Llandeilien supérieur. Les graptolites qui se trouvent à 38 m sous ce niveau sont plutôt des formes non caractéristiques de l'Arénigien-Llanvirnien, et ceux qui se trouvent à 36 m au-dessus correspondent à la zone à *Nemagraptus gracilis* du Llandeilien supérieur-Caradocien inférieur.

La répartition de *Protopanderodus* de l'Arenigien moyen à l'Ashgillien, dans le faciès de roches clastiques à grain fin du nord du Yukon et du sud-ouest des Territoires du Nord-Ouest et dans le faciès carbonaté de la dernière région, confirme la répartition connue du genre. Les espèces *Protopanderodus* étaient plus fréquentes au large des côtes, dans cette partie de la Laurentie où ces milieux extra-côtiers sont représentés par le groupe de Road River riche en roches clastiques. Par exemple, 0,2 % seulement des 9000 éléments des collections richmondiennnes de la bordure de la plate-forme carbonatée de la formation de Whittaker dans le sud-ouest des Territoires du Nord-Ouest appartient au genre *Protopanderodus* (Nowlan et al., 1988). Dans des couches équivalentes du groupe de Road River, aux rivières Blackstone et Peel dans le nord du Yukon, les faunes de conodontes comportent 13 % de *Protopanderodus*. Des couches plus anciennes contiennent des teneurs semblables. Au cours de l'Arénigien et du Llanvirnien, *Protopanderodus* représente environ de 11 à 56 % de la faune contenue dans les couches du groupe de Road River tandis qu'il se révèle rare ou absent dans le faciès carbonaté équivalent.

Protopanderodus s'est probablement différencié de *Drepanodus* avant l'Arénigien inférieur. Cette différenciation a pu se faire à partir d'une espèce de *Drepanodus* caractérisée par un appareil d'éléments qui constitue principalement une série transitionnelle quant à la courbure des cuspides, dont la transition de symétrie est moins évidente telle que montrée par la torsion des éléments (symétrie de torsion) et par une ornementation rarement à côtes, (symétrie des côtes), comparativement à une espèce de *Protopanderodus* dont la transition, quant à la symétrie des côtes, est plus apparente. Dans les premières espèces de *Protopanderodus*, cette symétrie se manifeste dans la position de l'ornementation sur des éléments à une et deux côtes et dans la torsion des éléments; les éléments de *Protopanderodus* présentent aussi une courbure variable.

La différence entre la symétrie apparente de *Drepanodus* et *Protopanderodus* est encore plus accentuée par la nature multiple et très sculptée de l'ornementation dans les espèces plus récentes de *Protopanderodus*. Même dans ces espèces à plusieurs côtes, la torsion et la courbure sont encore variables.

Drepanodus et *Protopanderodus* ont été classés dans le présent document dans la famille Protopanderodontidae, le premier faisant partie de la sous-famille Drepanodontinae et le second, de la sous-famille Protopanderodontinae.

Les Drepanodontinae sont caractérisés par une série (transitionnelle quant à la courbure des cuspides) d'éléments *a/b-c* (drépanodontiformes) à enroulement variable et ne comportant pas de côtes ou quelques rares côtes, et d'éléments *e* (scandodontiformes) sans côte; cette sous-famille comprend les genres *Drepanodus* et *Parapaltodus*. Les Protopanderodontinae, représentés seulement par *Protopanderodus*, comprennent des éléments *a/b-c* (acontiodontiformes) à enroulement variable (symétrie de torsion) à une ou plusieurs côtes au sein d'une série transitionnelle quant à la symétrie des côtes et à la courbure des cuspides de même que des éléments *e* (scandodontiformes) sans côte, à carène ou à côtes. Ces sous-familles se distinguent de la sous-famille des Drepanoistodinae de la famille des Drepanoistodontidae. Les Drepanoistodinae sont représentés par les genres *Drepanoistodus*, *Paltodus*, *Paroistodus* et peut-être *Besselodus* et sont caractérisés par une série transitionnelle quant à la courbure des cuspides d'éléments *a/b-c* (d'un à deux éléments drépanodontiformes distincts) à enroulement variable et d'un élément *e* (oistodontiforme) géniculé, lesquels peuvent se présenter avec ou sans côtes.

Les éléments *a/b-c* de *Protopanderodus* peuvent se distinguer, au moins en partie, de certaines espèces. Les éléments *a/b* et *c*, au sens strict, sont respectivement des éléments *a/b-c* asymétriques et symétriques. L'évolution d'éléments *a/b-c* postérieurs denticulés que l'on trouve dans les variétés symétriques et asymétriques ne se manifeste que dans *P. insculptus* et représente un trait distinctif de l'appareil le plus typique.

Protopanderodus représente deux lignées phylogénétiques qui se distinguent par leur degré d'ornementation (fig. 2). Le groupe ou la lignée comportant deux côtes comprend les éléments *a/b-c* avec au plus deux côtes latérales. Ce groupe inclut les espèces qui sont morphologiquement "transitionnelles" entre *Drepanodus* et *Protopanderodus*. Les espèces de la lignée à deux côtes sont *P. elongatus* Serpagli, *P. graeai* (Hamar), *P. leonardii* Serpagli, *P. parvibasis*, *P. rectus* (Lindström), *P. robustus*, *P.* sp. Löfgren et, du nord du Yukon, *P.* n. sp. A. Les éléments *e* des espèces de cette lignée varient : à une côte (*P. graeai*), lisse (*P. elongatus*, *P. robustus*, *P.* n. sp. A.), caréné (*P. rectus*) ou faiblement caréné et rainuré (*P. parvibasis*). La lignée à plusieurs côtes est représentée par les espèces dont les éléments *a/b-c* comportent deux côtes ou plus. Ces espèces sont *P. insculptus*, *P. gradatus* Serpagli, *P.? lee* Repetski, *P. liripipus*, *P. strigatus* Barnes et Poplawski, *P. varicostatus*, *P.* sp. Dzik et, du nord du Yukon, *P.* sp. B. Les éléments *e* de presque toutes ces espèces à plusieurs côtes sont visiblement rainurés sur leur face intérieure.

Les principaux changements d'évolution chez les Protopanderodontidae sont : l'augmentation du rapport des éléments à côte aux éléments sans côte d'une espèce telle que *Drepanodus arcuatus* Pander (qui diffère de *P.* n. sp. A dans la proportion des éléments sans côte à ceux qui en comportent) par rapport à une espèce antérieure de *Protopanderodus*; le prolongement des côtes vers la bordure aborale postérieure chez des espèces plus récentes de *Protopanderodus*; et la formation de deux lignées.

Les espèces à deux côtes *Protopanderodus elongatus* et *P. leonardii* sont les plus anciennes formes du genre. Elles existaient à l'Arénigien inférieur, au Texas, (Repetski, 1982) et la première espèce pourrait dater de la fin du Trémadocien. *P. rectus*, d'âge plus récent, pourrait être l'ancêtre direct de *P. graeai*, *P. parvibasis* et *P. robustus*. *Protopanderodus gradatus* pourrait constituer le lien entre les groupes à deux côtes et à plusieurs côtes. Son élément *c* comporte deux côtes tout comme ceux de la lignée précédente, mais ses éléments *a/b* et *e* sont semblables aux éléments de la lignée ultérieure. L'écart stratigraphique inférieur de *P. gradatus* et celui de l'espèce a deux côtes *P. rectus* coïncident. Les espèces à plusieurs côtes *P.* sp. Dzik, *P. varicostatus*, *P. liripipus* et *P. insculptus* forment une lignée divergente légèrement moins complexe que la lignée à deux côtes.

Six événements notables de l'évolution de *Protopanderodus*, dont certains peuvent être liés, du moins temporairement, aux événements eustatiques et autres événements fauniques, sont brièvement traités ci-dessous.

Les essais de corrélation des événements 1 (transition de *Drepanodus* à une ancienne espèce de *Protopanderodus* à deux côtes avant le début de l'Arénigien) et 2 (origine de la lignée à plusieurs côtes avant l'Arénigien moyen) à des modifications eustatiques du niveau de la mer sont entravés par le manque de précision dans la détermination du niveau de la première apparition des espèces des deux lignées. L'apparition de l'espèce à deux côtes, *P. elongatus*, a pu coïncider avec la transgression de l'Arénigien moyen. Cependant, *P. elongatus* sensu Repetski (1982) est peut-être en fait plus ancien et, si tel est le cas, il était présent au cours de la dernière phase de la transgression du Trémadocien supérieur. Les espèces à plusieurs côtes les plus anciennes, soit *P. gradatus* sensu Serpagli (1974) et *P. varicostatus* de Gastil et Miller (1981), correspondent toutes les deux à la transgression de l'Arénigien moyen.

Plusieurs espèces de *Protopanderodus* ont été retracées en Argentine, Texas, Utah et Nouveau-Mexique. Elles représentent probablement une faune du Pacifique qui comprenait deux espèces à deux côtes de l'Arénigien inférieur et, par la suite, deux espèces à plusieurs côtes de l'Arénigien moyen. L'apparition de ces deux formes précède celle des espèces *Protopanderodus* en Baltica et Iapetus, et semble indiquer que les lignées à deux et plusieurs côtes se sont développées dans l'ouest de l'océan Iapetus ou dans l'océan Pacifique (événement 3).

La divergence dans ces deux lignées (événement 4) a coïncidé avec une régression maximale à la fin de l'Arénigien et avec une transgression au début du Llanvirnien. La lignée à deux côtes s'est terminée (événement 5) au début du Caradocien au cours d'une importante transgression. L'événement 6, la différentiation de *P. insculptus* de *P. liripipus* du Caradocien supérieur et de l'Ashgillien inférieur constitue le dernier événement avant la disparition des deux espèces vers la fin de l'Ordovicien supérieur.

INTRODUCTION

Ordovician conodont collections from four sections of the Road River Group in northern Yukon (Fig. 1) have yielded relatively few elements of *Protopanderodus* (Table 1). The small faunas, however, are represented by five known species of *Protopanderodus*, and two unnamed species. Elements of *Protopanderodus* n. sp. A are similar to some previously assigned to *Drepanodus*; the reconstruction of the apparatus of this species is aided by a fused cluster of elements.

The sampled strata are rare limestone beds within sequences of graptolite-rich shale, calcareous shale and chert. The strata represent the basinal, fine clastic facies of the Blackstone Trough, trending west-southwest, and the nearby Richardson Trough, which trends north-northwest. Both troughs were bordered by platform-margin carbonate environments during the Ordovician and Silurian (Jackson et al., 1978; Lenz, 1982; Cecile and Norford, 1985).

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PROTOPANDERODUS IN NORTHERN YUKON

The Ordovician conodont/graptolite biostratigraphy from the Yukon sections is reported in Lenz and McCracken (1982), McCracken (1987) and McCracken and Lenz (1987). The following is a brief summary of the occurrences of *Protopanderodus* from northern Yukon.

The Blackstone River conodont fauna (sample BR:50.3 m; Table 1) contains both *Protopanderodus insculptus* (Branson and Mehl) and *P. liripipus* Kennedy et al. along with conodonts indicative of the lower part of the upper Richmondian, upper Ashgill *Gamachignathus ensifer* Zone (McCracken, 1987). The fauna occurs 3 m below graptolites of the tentative *Glyptograptus persculptus* Zone and 13.7 m above those of the *Paraorthograptus pacificus* Zone (Lenz and McCracken, 1982).

On the upper Peel River, a fauna (PR:358.1-362.7 m) was collected from a level 18.3 m below graptolites of the *Diplograptus decoratus* Zone (upper Llanvirn; Lenz and Chen, 1985), and 3.9 m above graptolites of the upper *Paraglossograptus tentaculatus* Zone (middle Llanvirn; Lenz and Jackson, 1986). *Protopanderodus parvibasis* Löfgren, *P. robustus* (Hadding), *P.* cf. *P. varicostatus* (Sweet and Bergström) and *P.* n. sp. A occur with conodonts representing the *Pygodus serra* Zone; the stratigraphic level of this fauna is regarded as middle Llanvirn.

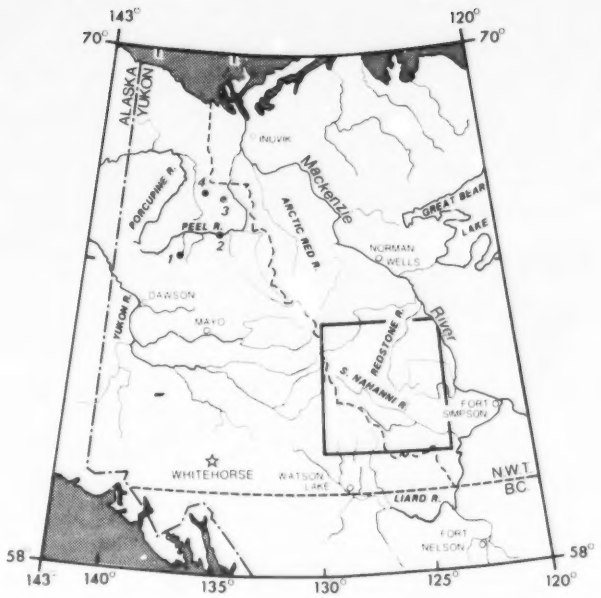


Figure 1. *Location of the four sections of this study: 1. Blackstone River (65°26'N, 137°20'W); 2. upper Peel River (65°53'N, 135°43'W); 3. south branch, Rock River (66°48'N, 136°16'W); 4. Tetlit Creek (66°44'N, 135°47'W). Rectangle shows approximate boundaries of study area of Tipnis et al. (1978), which is discussed in the text. (Figure modified from Nowlan et al., 1988)*

Protopanderodus insculptus and *P. liripipus* occur at upper Peel River (PR:452.6 m) within the upper Ashgill *P. pacificus* Zone, 1.9 m below the first occurrence of the lower Llandovery *Parakidograptus acuminatus* Zone, and are associated with an upper Richmondian (upper Ashgill) conodont assemblage that is indicative of the *G. ensifer* Zone (McCracken, 1987).

Associated with glossograptids, and 56 m below a rather undiagnostic collection of Llandeilo-Caradoc graptolites on Rock River, is a conodont fauna containing *Protopanderodus robustus*, *P.* cf. *P. varicostatus*, and species of other conodont genera. This fauna (RR:13 m) is probably upper Arenig or lower Llanvirn.

Higher in the Rock River section, *Protopanderodus insculptus* occurs at a level (RR:207 m) that is 13 m below graptolites of the lower Ashgill *Dicellograptus ornatus* Zone, and at a second level (RR:225 m) that is 5 m above graptolites of this zone and 7 m below graptolites of the *P. pacificus* Zone. There are no other diagnostic conodonts in the two samples; this interval could be as old as early Caradoc, based on the occurrence of *P. liripipus*, or as young as late Ashgill. Another fauna (RR:245 m) from a presumed debris bed within the Llandovery *Coronograptus gregarius* Zone at the Rock River section yielded Ordovician conodonts. The conodonts, primarily Upper Ordovician species, are mixed with a few Silurian species.

The poorly preserved conodont fauna from Tetlit Creek (TC:39 m) is from a bed 38 m above undiagnostic Arenig-Llanvirn graptolites and 36 m below graptolites representing the *Nemagraptus gracilis* Zone (upper Llandeilo-lower Caradoc). The conodonts include *Protopanderodus robustus*, *P.* cf. *P. varicostatus*, and the rare *P.* sp. B. The age range for this conodont sample is from early Llanvirn to late Llandeilo.

PALEOECOLOGY OF *PROTOPANDERODUS* IN THE NORTHERN CORDILLERA

Protopanderodus is found in Llanvirn – Ashgill strata of the basinal, fine-clastic facies of northern Yukon. The frequency of *Protopanderodus* elements in collections from the four sections is about 12 per cent. The relative abundance of the genus in the *Pygodus serra* Zone (upper Peel River), and in the upper Ashgill (upper Peel and Blackstone rivers) is about 15 and 13 per cent, respectively. No samples were collected from strata of the carbonate facies adjacent to the Road River Group. A comparison of faunas from the two lithofacies can, however, be made on the basis of previous work by Tipnis et al. (1978) and Nowlan et al. (1988) for the southwestern Northwest Territories.

The Road River Group at Section K of Tipnis et al. (1978) has a relative abundance of *Protopanderodus* elements that is about 11 per cent. This fauna is middle Arenig, based on the occurrence of *Prioniodus* (*Oepikodus*) *evae* Lindström (herein = *Oepikodus smithensis* Lindström). In higher strata of their Section K, *Protopanderodus* has a frequency of 56 per cent; this fauna includes *Amorphognathus variabilis* Sergeeva and is therefore late Arenig to early Llanvirn in age

TABLE 1

Distribution of *Protopanderodus* species and element abundance from the Road River Group, northern Yukon

GRAPTOLITE ZONE		*tentaculatus -decoratus*	pre- *?gracilis*	pre- *?Caradoc*	pre- *?ornatus*	*ornatus-pacificus*	*pacificus*	*?pacificus*	*gregarius*	
PROTOPANDERODUS **SPECIES**	**(TOTAL)**	**O-104254 PR:358.1 m**	**O-104293 TC:39 m**	**O-104271 RR:13 m**	**O-104274 RR:207 m**	**O-104275 RR:225 m**	**O-104256 PR:452.6 m**	**O-104267 BR:50.3 m**	**O-104279 RR:245 m**	**(TOTAL)**
P. insculptus										
a element	4	0	0	0	0	0	3	1	0	4
a/b element	13	0	0	0	1	1	10	1	0	13
c element	9	0	0	0	0	0	7	1	1	9
e element	2	0	0	0	0	0	2	0	0	2
gigantiform element	1	0	0	0	0	0	1	0	0	1
P. liripipus										
a/b element	10	0	0	0	0	0	9	0	1	10
c element	5	0	0	0	0	0	5	0	0	5
e element	2	0	0	0	0	0	1	1	0	2
gigantiform element	1	0	0	0	0	0	1	0	0	1
P. parvibasis										
c element	2	2	0	0	0	0	0	0	0	2
e element	1	1	0	0	0	0	0	0	0	1
P. robustus										
a/b element	15	1	5	9	0	0	0	0	0	15
c element	10	5	2	3	0	0	0	0	0	10
e element	7	4	0	3	0	0	0	0	0	7
P.* cf. *P. varicostatus										
a/b element	13	8	2	3	0	0	0	0	0	13
e? element	1	0	1	0	0	0	0	0	0	1
gigantiform element	1	1	0	0	0	0	0	0	0	1
***P.* n. sp. A**										
a/b element	4	4	0	0	0	0	0	0	0	4
c element	7	7	0	0	0	0	0	0	0	7
e element	1	1	0	0	0	0	0	0	0	1
***P.* sp. B**										
a/b element	1	0	1	0	0	0	0	0	0	1
c element	1	0	1	0	0	0	0	0	0	1
***Protopanderodus* indet.**										
a/b-c element	4	0	0	0	0	1	1	1	1	4
(TOTAL)	**115**	**34**	**12**	**18**	**1**	**2**	**40**	**5**	**3**	**115**

Sample numbers consist of GSC locality numbers, and the section locality abbreviation and collection level in metres.
Samples and graptolite zones are listed in ascending stratigraphic order.
Sample PR:358.1 m is from a bed within a 1.8 m unit of carbonate; the complete interval is 358.1-362.7 m.
Sample RR:245 m is from within the Llandovery *Coronograptus gregarius* Zone. The Ordovician conodonts in this sample had been reworked.

(values are calculated from Tables II and III, respectively, of Tipnis et al., 1978). The relative abundance of *Protopanderodus* is about 13 per cent in the *P. serra* Zone of locality 5 (Tipnis et al., 1978, Table IV). About 8 per cent of the fauna of the *Amorphognathus superbus* Zone (late Caradoc – early Ashgill) is *Protopanderodus* (*ibid.*, Table V).

The Broken Skull, Sunblood, Esbataottine and Whittaker formations represent the carbonate facies in southwestern Northwest Territories. Strata of the Broken Skull Formation were described by Tipnis et al. (1978, p. 45) as being close to the western edge of the Ordovician shelf margin, where they grade into strata of the fine-clastic facies of the Selwyn Basin. In the upper Tremadoc to lower Arenig strata containing Fauna D and Fauna E, the relative abundance of *Protopanderodus* is about 3 per cent (Tipnis et al., 1978, Table VI; samples D215-D485). *Protopanderodus* represents about 4 per cent in strata containing Fauna 1 (middle Arenig) of the Broken Skull Formation (*ibid.*, Tables VI, VII; samples D555-D825). Collections in two samples from overlying strata of the same formation and section, interpreted as possibly Fauna 2 (middle Arenig), contain about 9 per cent *Protopanderodus* (*ibid.*, p. 55, Table VII; samples D840, D860). *Protopanderodus* (about 3 per cent) is present only in the basal sample H0 of the succeeding Sunblood Formation. The remaining 48 samples (identified as containing Faunas 2-8) from the Sunblood Formation do not contain elements of *Protopanderodus*. The 18 samples of the Esbataottine Formation (Faunas 6-8), and 36 samples of the Whittaker Formation (Faunas 8-?10) are similarly lacking in elements of *Protopanderodus* (*ibid.*, Tables XI-XV).

Only a few (0.2 per cent) of the more than 9000 elements in the Fauna 12 collections from the carbonate sequence of the upper Whittaker Formation at Avalanche Lake in southwestern Northwest Territories are *Protopanderodus*. These Richmondian strata were considered by Nowlan et al. (1988) to represent the transition from the carbonate platform facies to the outer detrital basinal facies.

The distribution of *Protopanderodus*, from the middle Arenig to the Ashgill, in the fine-clastic facies of northern Yukon and southwestern Northwest Territories, and the carbonate facies of southwestern Northwest Territories, conforms with the known distribution of the genus. Species were more common in the offshore marine environments of Laurentia, which are represented by the clastic-rich Road River Group (see *Protopanderodus* Evolutionary Events, below.)

EVOLUTION OF *PROTOPANDERODUS*

Protopanderodus had probably evolved from *Drepanodus* by the early Arenig (see *Protopanderodus* Phylogeny). Evolution may have been from a species with an apparatus of elements that primarily consist of a cusp-curvature transition series, with a less obvious symmetry transition character displayed by the torsion of the elements (torsion-symmetry) and, rarely, costate ornamentation (costae-symmetry), to a species where the costae-symmetry transition is more apparent. In early *Protopanderodus*, this symmetry is shown through the position of ornamentation on uni- and bi-costate elements, and the torsion of the elements; elements of *Protopanderodus* also exhibit variable curvature.

The difference between the apparent symmetry in *Drepanodus* and *Protopanderodus* is further exaggerated by the multiple and highly sculpted nature of ornamentation in younger species of *Protopanderodus*, such as *P. varicostatus* (Sweet and Bergström). Even in these multicostate species, variable torsion and curvature are still present.

Both *Drepanodus* and *Protopanderodus* are regarded herein as belonging to the Family Protopanderodontidae. Even though elements of early bicostate species of *Protopanderodus* can be confused with those of *Drepanodus*, it is reasonable to separate the two genera into two subfamilies: Protopanderodontinae and Drepanodontinae (see remarks about Protopanderodontinae under Systematic Paleontology).

As the degree of ornamentation is one of the most notable differences between *Drepanodus* and *Protopanderodus*, particularly the multicostate species, it is used as the principal diagnostic feature for the two subfamilies. The presence of striae has been used in a previous diagnosis of *Protopanderodus*, but herein is considered to be an unreliable criterion.

The apparatus of the type species of *Drepanodus*, *Drepanodus arcuatus* Pander (sensu Löfgren, 1978), comprises *a/b-c* elements, represented by a series of variable drepanodontiform elements (first transition series) and an *e*, or scandodontiform element (the sole element of the second transition series). *Protopanderodus* has a homologous apparatus with *a/b-c* (acontiodontiform) and *e* (scandodontiform) elements. *Drepanodus arcuatus* from Argentina (Serpagli, 1974) and from the lower Fillmore Formation and underlying strata of Utah (Ethington and Clark, 1982) may lack the distinctive *e* element (see remarks about *Protopanderodus* n. sp. A below).

The *a/b-c* elements of *Protopanderodus* can at least be partly differentiated in some species. The *a/b* and *c* elements in the simplest sense are, respectively, the asymmetrical and symmetrical acontiodontiform elements. The concept of symmetry is probably best used in a rather broad sense, to encompass what have been termed subsymmetrical elements.

Whether the *a/b* elements can be further divided into separate groups is questionable. Are the *a/b* elements of *Protopanderodus insculptus* (Branson and Mehl) from northern Yukon that have three costae, homologous with elements in the *a* position, and are those asymmetrical elements that have four costae, homologous with elements in the *b* position? *Protopanderodus liripipus* Kennedy et al. (herein) has *a/b* elements that vary from bicostate (two costae on one face) to quadri- and quinquecostate – how are these to be interpreted? A potential *a* element for a close relative to *P.* n. sp. A (herein) is also speculated upon under the remarks about this species (see also remarks about *Protopanderodus* under Systematic Paleontology).

The development of a posteriorly denticulated acontiodontiform element in the *Protopanderodus* apparatus is the most significant departure from the typical *Drepanodus* apparatus. Indeed, it represents a notable step in the evolution of *Protopanderodus*. The only denticulate species, *P. insculptus*, was originally illustrated with two of the three cotypes being denticulate. Branson and Mehl (1933, p. 125) noted that in some specimens the denticle is absent.

The denticulate element has been reported from a number of localities (see *Protopanderodus insculptus*, below) but it commonly seems to be a rare form; in one sample from northern Yukon (PR:452.6 m), the ratio of denticulate to adenticulate *a/b-c* elements is 3:20. Interestingly, the ratio in an unpublished collection (GSC C-134208) from the Irene

Bay Formation of Middle Island, Northwest Territories is 11:7. In this sample, as in the collections from northern Yukon, both symmetrical and asymmetrical varieties of denticulate elements are present. Although the elements from Middle Island are well preserved (albeit debris covered), this is probably not the reason for the high abundance of denticulate elements. If preservation is the prime factor in determining the frequency of denticulate elements, then it should be possible to identify broken denticles, or at least denticle bases in samples that yield adenticulate but few denticulate varieties.

A question arises – do the denticulate elements assigned to *Protopanderodus insculptus* represent a species distinct from one with adenticulate elements, even where they occur rarely, or do they represent a modification of the existing apparatus of *P. insculptus* (with a low frequency of denticulate elements), and an isolated or later reversal of this ratio in certain paleogeographic areas?

As well as this form of denticulation, the addition of costae, intercalation or bifurcation of secondary costae, and the appearance of the gigantiform elements are usually rare events. The quinquecostate element in *Protopanderodus liripipus* is an example of an element with "additional" costae, acontiodontiform elements of this species usually have three or four costae. A figured element of *Acontiodus arcuatus* Lindström s.f. (generic affinity of the type series is uncertain), an element of *P. reclinatus* (Lindström)? of Barnes and Poplawski (1973; see *P.* n. sp. A, herein) an element of *P. robustus* (Hadding) sensu Bradshaw (1969; see *P. robustus*, herein), and a gigantiform element of *P. insculptus* (Pl. 3, fig. 14) all have secondary costae. Gigantiform elements are reported herein as part of the apparatuses of *P. insculptus*, *P. liripipus* and *P.* cf. *P. varicostatus*, although their position within the apparatus is not known.

The term "gerontic" is used to describe "aberrant" forms with additional or secondary costae, and the gigantiform elements; it should not be applied to the denticulate elements since they are found in a range of presumably ontogenetic stages. However, except for the very large robust forms of gigantiform elements, which retain the beautifully sculpted ornamentation, it is probably an inadequate or inappropriate term. These characteristics may be recessive rather than due to advanced ontogeny.

PHYLOGENY OF *PROTOPANDERODUS*

Species of *Protopanderodus* are herein placed into two groups according to the degree of ornamentation; these groupings are regarded as representing phylogenetic lineages. Figure 2 illustrates the stratigraphic ranges and suggested relationships of species of the two groups. The Arenig to Ashgill biostratigraphic zones and subzones mentioned below are shown in this figure.

Lineages

The bicostate group or lineage (Fig. 2) has acontiodontiform (*a/b-c*) elements with two or less lateral costae. This group includes species that are regarded as morphologically "transitional" between *Drepanodus* and *Protopanderodus*. Species of the bicostate group are: *P. elongatus* Serpagli, *P. graeai* (Hamar), *P. leonardii* Serpagli (the *e* element, i.e. scandodontiform, is unknown), *P. parvibasis* Löfgren, *P. rectus* (Lindström), *P. robustus* (Hadding), *P.* sp. Löfgren (*e* element unknown) and *P.* n. sp. A (herein). *Protopanderodus graeai* has an *e* element that is unicostate (prominent costa on inner lateral face); the other species have *e* elements with an inner face that is either smooth (*P. elongatus*, *P. robustus*, *P.* n. sp. A), carinate (*P. rectus*), or weakly carinate and grooved (*P. parvibasis*).

The multicostate lineage (Fig. 2) comprises *Protopanderodus insculptus* (Branson and Mehl), *P. gradatus* Serpagli, *P.*? *leei* Repetski, *P. liripipus* Kennedy et al., *P. strigatus* Barnes and Poplawski, *P. varicostatus* (Sweet and Bergström) s.l., *P.* sp. Dzik (1983; *e* element unknown) and *P.* sp. B (herein; *e* element unknown). These species have multicostate (two or more costae) *a/b-c* elements, and except for *P. strigatus*, all known *e* elements are noticeably grooved on the inner face. The *e* element of *P. strigatus* is similar to the *e* elements in some species of the bicostate group in that the inner face is carinate.

Protopanderodus? *leei*, if indeed a species of *Protopanderodus*, is morphologically "transitional" between bicostate and multicostate species. It must be included within the multicostate group since some elements possess two to four costae. *Protopanderodus*? *leei* has an *e* element with smooth faces as in bicostate species, but also includes *a/b-c* elements with a lateral costa on each face, and two closely spaced posterolateral costae, which bound a concave posterior face (Repetski, 1982). The short and expanded base, erect to slightly proclined cusp, rounded anterior face and keel-like lateral costae of the *a/b-c* element of *P.*? *leei* are features found on elements of *Semiacontiodus*.

In a similar sense, *Protopanderodus gradatus*, *P. strigatus*, and *P.* sp. B (from northern Yukon) also are "transitional" in morphology. Their *a/b* elements are multicostate, but the *c* elements are bicostate (see remarks about *P.* sp. B, below).

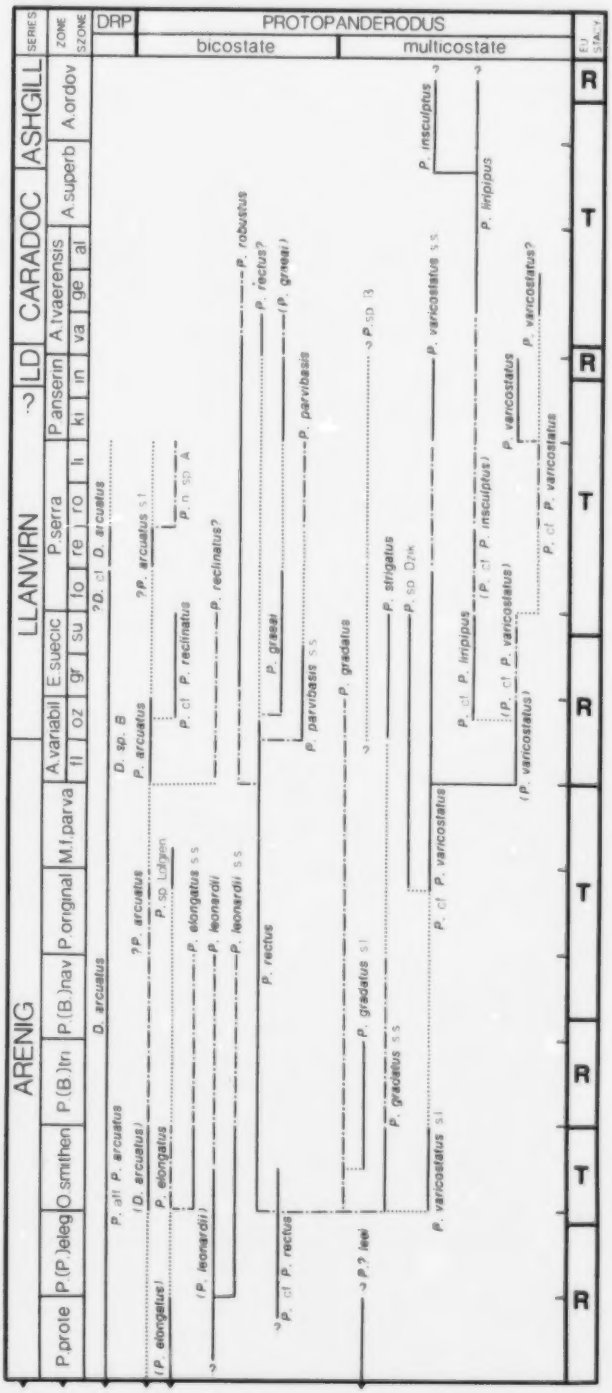
The increase in the ratio of costate to acostate elements from *Drepanodus arcuatus* Pander to an early species of *Protopanderodus*, the extension of costae toward the posterior aboral margin in later species of *Protopanderodus*, and the development of bicostate and multicostate lineages are the principal evolutionary changes. Similar element morphology and ranges of some bicostate species make interpretation of their evolutionary lineages tenuous. The bicostate forms represent divergent evolution; the multicostate species, at least the younger ones, are part of a clearer succession (Fig. 2).

Bicostate species

Protopanderodus probably evolved from early species of *Drepanodus*, such as *D. arcuatus*, by further development of costae (Stouge, 1984). *Drepanodus arcuatus* and *P.* n. sp. A are quite similar; they differ primarily in the proportion of costate to acostate elements.

Costae play a significant role in the present interpretation of *Protopanderodus*, and there are differences between costae on elements of *Drepanodus arcuatus*, *P.* n. sp. A and other *Protopanderodus* species. The costae on elements of *D. arcuatus* and *P.* n. sp. A terminate high on the base rather than extending close to, or ending at, the aboral margin as they do in other species of Protopanderodus.

Forms similar to *Protopanderodus* n. sp. A occur elsewhere in the middle Arenig (*Prioniodus* (*Oepikodus*) *smithensis* Zone; Landing, 1976; herein = *O. smithensis* Zone), and in the upper Arenig to lower Llanvirn (Tipnis et al., 1978; Stouge, 1984). *Drepanodus arcuatus* of Löfgren occurs in the lowest Arenig *Paroistodus proteus* Zone of Sweden and ranges through to at least the *Pygodus serra* Zone (Fig. 2). If one of these is the direct ancestor of later species, then *Protopanderodus* must have evolved from *Drepanodus* by the early Arenig because of the occurrence of *P. elongatus* and *P. leonardii* in Argentina (Serpagli, 1974) and western Texas (Repetski, 1982) (see *Protopanderodus* Evolutionary Events).



The bicostate species *Protopanderodus elongatus* and *P. leonardii* are the oldest forms; both occur in the strata of west-central Argentina that contain Fauna B and Fauna C sensu Serpagli (1974). Serpagli's faunas must not be confused with the faunas of Ethington and Clark (1971). These middle Arenig strata were assigned to the *O. smithensis* Zone (Serpagli's Fauna B), and the *Prioniodus* (*Baltoniodus*) *triangularis*, and possibly the ?*P.* (*B.*) *navis* zones (his Fauna C), although the last fauna does not contain index species. *Protopanderodus leonardii* has a greater lower limit, possibly to the *Prioniodus* (*P.*) *elegans* Zone (Serpagli, 1974). The first appearance of both species in the western Texas area may be in the early Arenig; *P. elongatus* may range as low as late Tremadoc (Repetski, 1982). The bicostate species, *Protopanderodus rectus*, first appears in the *O. smithensis* Zone of Sweden; *P.* cf. *P. rectus* (sensu Repetski, 1982) from Texas may also be older (Fig. 2).

Protopanderodus sp. Löfgren is known only from the upper *Paroistodus originalis* to *Microzarkodina flabellum parva* zones of Sweden. This range is above those of *P. elongatus* and *P. leonardii* (which are not known in Sweden), is concurrent with part of the range of *P. rectus*, and well below the first appearance of *P. graeai*, *P. parvibasis*, and *P. robustus*. The stratigraphic position of the occurrence in Sweden may imply evolution of *P.* sp. Löfgren from *P. rectus*, but the costae are not as strong nor as basally long as they are on *a/b-c* elements of *P. rectus*. The morphology of *P.* sp. Löfgren could imply a relationship with species such as the older *P. elongatus*. It must be noted, however, that there is a stratigraphic gap between the occurrences of these two species.

Figure 2. *Stratigraphic ranges and evolution of* ***Protopanderodus*** *and* ***Drepanodus*** *species, and Ordovician eustatic phases. Some species are junior synonyms (see text for details). Stratigraphic ranges of species named in the figure are summarized in the Appendix. Zonal scheme is from Bergström (1971, 1983), Lindström (1971) and Löfgren (1978). The position of the* ***A. superbus–A. ordovicicus*** *zonal boundary is sensu Bergström (1983, p. 51). LD, Llandeilo Series; DRP,* ***Drepanodus****.*

Symbols for zones: P. prote, ***Paroistodus proteus****; P. (P.) eleg,* ***Prioniodus (P.) elegans****; O. smithen,* ***Oepikodus smithensis*** *(=P. (O.) evae); P. (B.) tri,* ***P. (Baltoniodus) triangularis****; P. (B.) nav,* ***P. (B.) navis****; P. original,* ***Paroistodus originalis****; M. f. parva,* ***Microzarkodina flabellum parva****; A. variabil,* ***Amorphognathus variabilis****; E. suecic,* ***Eoplacognathus suecicus****; P. serra,* ***Pygodus serra****; P. anserin,* ***P. anserinus****; A. tvaerensis,* ***Amorphognathus tvaerensis****; A. superb,* ***A. superbus****; A. ordov,* ***A. ordovicicus****.*

Symbols for subzones (SZONE): fl, ***A. variabilis – M. flabellum****; oz,* ***A. variabilis – M. ozarkodella****; gr,* ***E. suecicus – Scalpellodus gracilis****; su,* ***E. suecicus – Panderodus sulcatus****; fo,* ***E. foliaceus****; re,* ***E. reclinatus****; ro,* ***E. robustus****; li,* ***E. lindstroemi****; ki,* ***A. kielcensis****; in,* ***A. inaequalis****; va,* ***P. (B.) variabilis****; ge,* ***P. (B.) gerdae****; al,* ***P. (B.) alobatus****.*

Under the eustacy column, R and T represent regressive and transgressive phases, respectively. Sources are: Barnes (1984) for the Arenig to lower Llanvirn; Fortey (1984) for the Llanvirn to Caradoc; and Brenchley and Newall (1984) for the Ashgill.

An evolutionary lineage beginning with *Protopanderodus rectus* and including *P. graeai*, *P. parvibasis* and *P. robustus*, is suggested by their element morphology and successive appearances (Fig. 2), the last three species finally co-occurring by the early Llanvirn. Except for *P. parvibasis*, species of this lineage range into the Caradoc. Nowlan (1981a) reported *P. graeai* and *P. rectus*? from the *Prioniodus* (*Baltoniodus*) *variabilis* Subzone, and Burrett et al. (1983) found *P. robustus* in the younger *Prioniodus* (*B.*) *gerdae* Subzone (see *Protopanderodus* Evolutionary Events section, below).

All four species occur in Swedish strata (Löfgren, 1978) but *Protopanderodus parvibasis* is the only species that directly succeeds *P. rectus* in the lower *Amorphognathus variabilis – Microzarkodina ozarkodella* Subzone. A small stratigraphic gap exists between *P. rectus* and *P. graeai*; the latter has its first appearance in the upper *A. variabilis – M. ozarkodella* Subzone. *Protopanderodus robustus* is the last of these species to appear in Sweden. It occurs first in the lower *Eoplacognathus suecicus – Scalpellodus gracilis* Subzone. These occurrences suggest that *P. rectus* is a direct ancestor of *P. parvibasis*, and from this, Löfgren (1978) thought that *P. graeai* and *P. robustus* must have evolved from *P. rectus*, outside her study area.

The first appearance of *Protopanderodus robustus* may be lower, as implied by the studies of Nowlan and Thurlow (1984), who reported this species from Whiterockian (uppermost Arenig – lower Llanvirn) strata, and by Stouge (1984; *A. variabilis – M. ozarkodella* Subzone). The last occurrence of *P. graeai* and *P. rectus*, and *P. parvibasis* may be higher, as indicated by the report of Nowlan (1981a), and the present study, respectively. Nowlan identified *P. graeai* and *P. rectus*? from the lower Caradoc (*P.* (*B.*) *variabilis* Subzone) in New Brunswick; *P. parvibasis* is identified from the *P. serra* Zone in northern Yukon.

Apart from the similar bicostate nature and the strong, basally long costae on the *a/b*-*c* elements, there are several other morphological similarities among the four species. *Protopanderodus robustus* is morphologically closest to *P. rectus* and the asymmetrical acontiodontiform (*a/b*) elements of *P. robustus* are virtually indistinguishable from those of *P. rectus* (Lofgren, 1978). The *c* (symmetrical acontiodontiform) element of *P. parvibasis* resembles the same element of *P. rectus* and *P. robustus*, but has a shorter oral margin or base. The *c* element of *P. graeai* is easy to distinguish from the homologous elements of the other species because of its long base.

The *e* (scandodontiform) element of *Protopanderodus rectus* has an inner face that is carinate, as in the homologous element of *P. parvibasis*, although this element in the latter species also has a shallow groove along the anterior side of the carina. Some upper Arenig *e* elements of *P. rectus* have a sharper carina or costa and thus are similar to the homologous element of *P. graeai*.

The ratio of *c* to *e* elements is about 3:1 for both *Protopanderodus parvibasis* and *P. robustus*. *Protopanderodus graeai* and relatively old forms of *P. rectus* have a ratio of 2:1, whereas younger specimens of *P. rectus* have a ratio of 3:1.

Protopanderodus robustus may be directly related to either *P. parvibasis* or *P. graeai*. However, the small stratigraphic gap between *P. rectus* and *P. graeai* in Sweden, and the possibility that *P. robustus* may be older (sensu Nowlan and Thurlow, 1984; Stouge, 1984) than the Swedish forms suggests that this evolutionary scenario is not the only possibility. Furthermore, from the element morphology, element ratios, and the close stratigraphic occurrences, a late Arenig or early Llanvirn evolutionary radiation is implied, with *P. rectus* as the parent stock of the other three species.

The arguments for *Protopanderodus rectus* being the direct ancestor of all three bicostate *Protopanderodus* species are as follows:

1. *Protopanderodus graeai*. The element ratio is identical to that in early forms of *P. rectus*; the *e* element is costate like some *e* elements of *P. rectus*; a very small stratigraphic gap exists between the last occurrence of *P. rectus* and the first appearance of *P. graeai* in Sweden; the base of the *c* element is markedly long compared with the same element of *P. parvibasis*, which is the most obvious relative if only stratigraphic data are considered.

2. *Protopanderodus parvibasis*. The element ratio is identical to that of later forms of *P. rectus*; the *e* element is carinate like that of *P. rectus*; *P. parvibasis* immediately succeeds *P. rectus* in Sweden.

3. *Protopanderodus robustus*. This species is morphologically closest to *P. rectus*; *a/b* elements and element ratios are identical to those of *P. rectus*; a stratigraphic gap between *P. rectus* and *P. robustus* exists in Sweden, but elsewhere, the first appearance of *P. robustus* may be lower.

The *e* elements of *Protopanderodus graeai* and *P. parvibasis* both have ornamentation somewhat similar to that in multicostate *Protopanderodus* species. The evolutionary significance of this is not known, but it suggests parallel evolution since the multicostate lineage is well represented by *P. varicostatus* s.l. at the same stratigraphic level.

Multicostate species

It is tempting to suggest that the morphologically intermediate species, *Protopanderodus*? *leei*, may be a link between early bicostate and multicostate species but, as mentioned above, its generic assignment is questionable, and its descendants, if any, are unknown. The upper Tremadoc or lower Arenig *P.*? *leei* occurs in strata of the western Texas area (Repetski, 1982) and South Korea (Lee, 1970).

An alternative link to the bicostate and multicostate groups is *Protopanderodus gradatus*. Its *c* element is bicostate, as are the *c* elements of the former group, but the *a/b* and *e* elements are similar to the same elements of the multicostate group. The lower stratigraphic ranges of *P. gradatus* and *P. rectus* are concurrent (Fig. 2).

Repetski (1982) reported the occurrence in western Texas of *Protopanderodus elongatus*, *P. leonardii*, *P.* cf. *P. rectus* (all bicostate species), and the multicostate *P. gradatus*. The earliest occurrence of *P. gradatus* is within the *O. smithensis* Zone of Argentina. However, it could have appeared earlier, as indicated by an occurrence in northern Scotland (middle or upper Canadian to lower Whiterockian; Bergström and Orchard, 1985). Repetski (1982) noted that the elements of *P. gradatus* and *P. rectus* were similar, and suggested that the two species are closely related. Of these four species, only *P. rectus* s.l. is not known from Argentina (Serpagli, 1974).

Protopanderodus varicostatus sensu Gastil and Miller (1981) is a species from a miogeoclinal setting that is west of

a megashear Pacific Plate boundary in northwestern Mexico. All of these species from Argentina, Mexico and Texas are of similar age (see Fig. 2) and may represent an evolutionary radiation within a Pacific conodont fauna (see *Protopanderodus* Evolutionary Events).

A slightly less complex divergent lineage is that of the multicostate species *Protopanderodus* sp. Dzik, *P. varicostatus* s.l., *P. liripipus* and *P. insculptus* (Fig. 2). An ancestor of these may be the lower Arenig *P.? leei* (but see above), or the middle Arenig *P. gradatus*. Stouge (1984) suggested that the close similarities of *P. gradatus* and *P. strigatus* indicate that they are related. However, there may be a considerable gap between their ranges. The similar *P.* sp. B of northern Yukon occurs stratigraphically higher than both species. A direct link among these three species is tenuous because of a lack of data from intervening strata.

The *e* element of the multicostate *Protopanderodus strigatus* shares a similar ornamentation with the *e* element of the bicostate species *P. rectus*. The upper limit of *P. rectus* is lowest Llanvirn in Sweden (lower part of the *A. variabilis – M. ozarkodella* Subzone; Löfgren, 1978). The lower limit of *P. strigatus* is from about the middle of the same subzone (Stouge, 1984). The similar *e* element morphology and stratigraphic occurrences could indicate that *P. strigatus* alternatively may have evolved from the bicostate lineage rather than the multicostate *P. gradatus*, as is shown in Figure 2; if so, its multicostate nature would thus be an example of parallel evolution.

The transition to *Protopanderodus* cf. *P. varicostatus* must have occurred by the upper Arenig *Paroistodus originalis* Zone (Löfgren, 1978), if not in the middle Arenig (i.e. *P. varicostatus* sensu Gastil and Miller, 1981). The *Protopanderodus varicostatus* s.s. is younger, appearing first in the uppermost Llanvirn – Llandeilo *Pygodus anserinus* Zone. *Protopanderodus* cf. *P. varicostatus* may be a morphologically, but not biogeographically (see Systematic Paleontology) distinct species from *P. varicostatus* s.s., and their ranges may partially overlap from the late Arenig to the late Llanvirn (Fig. 2).

Protopanderodus sp. Dzik (1983, Fig. 3:32) from the Oil Creek Formation of Oklahoma has at least three forms of *a/b-c* elements: 1) symmetrical bicostate; 2) asymmetrical tricostate; and 3) symmetrical quadricostate. The last form is unusual in that the anterior face is flat to concave rather than being narrowly convex. Dzik (1983) illustrated this species from a level about that of the *O. smithensis* to *P. originalis* zones, but Sweet and Bergström (1976, p. 147) place the strata it occurs in at a higher level, which is equivalent to the upper *P. originalis* to *E. suecicus* zones. Both levels are within the lower range of *P.* cf. *P. varicostatus* sensu Löfgren (1978); the two species are probably closely related (Fig. 2).

Protopanderodus liripipus s.l. could have developed from *P. varicostatus* s.l. as early as the *A. variabilis – M. ozarkodella* Subzone (Stouge, 1984; see *Protopanderodus* Evolutionary Events); *P. varicostatus* s.s. and *P. liripipus* s.s. coexisted possibly from the middle Llanvirn *P. serra* Zone (Tipnis et al., 1978), or younger *P. anserinus* Zone (Repetski and Ethington, 1977) until the lower Caradoc *Prioniodus (Baltoniodus) gerdae* Subzone (Fig. 2).

Protopanderodus liripipus and *P. insculptus* coexisted during the Ashgill *Amorphognathus ordovicicus* Zone; the latter species of *Protopanderodus* must have evolved from *P. liripipus* in the upper *Amorphognathus superbus* Zone (see Figure 2 and *Protopanderodus* Evolutionary Events section, below).

There are notable morphological similarities among some multicostate species. Some *a/b-c* elements of *Protopanderodus* cf. *P. varicostatus* of northern Yukon have short, unkeeled and pointed bases like some *a/b-c* elements of *P. liripipus*. The groove on the inner face of the *e* element of *P.* cf. *P. varicostatus*, *P.* cf. *P. liripipus* of Stouge (1984) and *P. liripipus* s.s. is more anterior than medial, as it is in the *e* element of *P. varicostatus* s.s. and *P. insculptus*.

A denticulated acontiodontiform element, as found in *Protopanderodus insculptus*, is not present in any other species of *Protopanderodus*. It represents a significant modification of elements in the *Protopanderodus* apparatus by Late Ordovician time (see Evolution of *Protopanderodus*).

OTHER "*PROTOPANDERODUS*" SPECIES

Not all species identified elsewhere as *Protopanderodus* are presented in the above discussion. Figured and unfigured types and specimens of species assigned to *Protopanderodus* by Barnes and Poplawski (1973) have been viewed; some of these should not be regarded as species of *Protopanderodus*.

Protopanderodus asymmetricus Barnes and Poplawski was interpreted as a species of *Juanognathus* by Bergström (1979), and questionably as a species of *Glyptoconus* by Dzik (1983). The elements are finely striated like the type species of *Glyptoconus*. Assignment of *P. asymmetricus* to *Juanognathus* may be preferred because of the well developed lateral keels and albid nature of the elements (holotype and some paratypes have white matter at the tip of the cusp; paratypes GSC 30294, 30296 have white matter throughout the entire cusp). Alternatively, the species may represent a new genus.

The figured specimens of *Protopanderodus* cf. *P. giganteus* (Sweet and Bergström) sensu Barnes and Poplawski comprise one symmetrical and two asymmetrical elements. The asymmetrical elements (Barnes and Poplawski, 1973, Pl. 1, fig. 4; unfigured specimen GSC 30309) are twisted and have a short base and recurved cusp. The outer and inner faces have about the same number of equally strong costae that are restricted to the area between mid-cusp and the posterior margin (total of about 14 on the large, and 8 on the small specimens). The symmetrical element (unfigured specimen GSC 30308) is not twisted, has about seven costae on each lateral face, a relatively long base and a proclined cusp.

These elements are tentatively regarded herein as a species of *Scolopodus* (sensu Stouge, 1984). The asymmetrical elements are more recurved, and more costate than homologous elements of *S. rex* Lindström, and *S. oldstockensis* Stouge, respectively. The generic assignment has to be questioned since the elements are broken at the proximal end of the cusp and therefore, it is not known if the elements are entirely hyaline. The large, bilaterally symmetrical *S. giganteus* s.f. of Landing (1976), and asymmetrical form species of Nowlan (1981a; type viewed) may be conspecific.

The type specimens of *Scolopodus giganteus* s.f. are large and have a similar arrangement of costae. They differ in having a rather long base and a notch-like indentation at the antero-aboral corner; these features are typical of elements in some species of *Protopanderodus*. Large, costate elements have probably been incorrectly assigned to *S. giganteus* s.f.; although they are usually found with elements of *Protopanderodus*, the elements are not necessarily all congeneric.

Protopanderodus? *tricarinatus* Barnes and Poplawski is characterized by well developed lateral keels and a narrow posterior ridge, all of which contain white matter. The ridge in the unfigured paratypes (GSC 30329, 30330) has a shallow, medial groove in the area of curvature. That is, the posterior face is bicostate as in elements of *Glyptoconus* (sensu Dzik, 1983), and some species of *Semiacontiodus* and *Staufferella*. The outline of the base is quite different from bases in the three genera and therefore a generic interpretation will not be made, except that the species does not belong to *Protopanderodus*.

Protopanderodus n. sp. Barnes and Poplawski was described as having a symmetry transition series of acodontiform, distacodontiform and acontiodontiform elements. One acostate element (unfigured specimen GSC 30302) has a wide base, sharp anterior and posterior edges and an erect and laterally twisted cusp; this could be regarded as an *a* element.

The distacodontiform (*b*) elements of *Protopanderodus* n. sp. Barnes and Poplawski (1973, Pl. 2, figs. 5, 6, Fig. 2D; unfigured specimens GSC 30304, 30306) and acontiodontiform (*c*) elements (*ibid.*, Pl. 2, fig. 12, unfigured specimens GSC 30303, 30305) have variably keeled lateral faces, costate posterior margins and, except for one specimen (*ibid.*, Pl. 2, fig. 6), have a smooth and convex anterior face. This last specimen has a keel that extends from the base to the proximal part of the cusp; the entire anterior face is otherwise convex. One *c* element of *P.* n. sp. Barnes and Poplawski (*ibid.*, Pl. 3, fig. 10) differs from the other *b-c* elements in that the posterior face is bicostate and the basal outline is rounded, not subtriangular.

The lateral keels and convex anterior face of *Protopanderodus* n. sp. Barnes and Poplawski are suggestive of *Glyptoconus* (sensu Dzik, 1983), *Juanognathus*, *Semiacontiodus* and *Staufferella*. The costate posterior margin of the *b* and *c* elements, and the wide base and erect nature of the *a* element, are characters found in species of *Semiacontiodus*.

The affinity of *Protopanderodus*? n. sp. Barnes and Poplawski (1973, Pl. 2, fig. 9) is not known. The short, undenticulated lateral processes, and the long process-like base are similar to those of *Oepikodus*? n. sp. Repetski (1982). The posterior edge of the cusp and oral edge of the base are thin and keel-like.

Protopanderodus? sp. Barnes and Poplawski (1973, Pl. 1, fig. 15) was assigned to *Juanognathus variabilis* Serpagli by Bergström (1979, p. 303), and, with a conferred designation, by Repetski (1982).

Protopanderodus cornuformis (Sergeeva) sensu Lindström (1971, p. 32) was assigned to *Scolopodus* by Löfgren (1978), and to *Semiacontiodus* by Dzik (1983) and Stouge (1984).

Protopanderodus latus van Wamel (1974) and *P. longibasis* (Lindström), both from the lower Arenig, seem to lack lateral costae, although they have the fine longitudinal striations that were part of the original generic diagnosis (see emended diagnosis under Systematic Paleontology, below). Without lateral costae, these two species cannot be regarded as species of *Protopanderodus*, as interpreted herein. Dzik (1976) selected the former as type species of *Scalpellodus*; Serpagli (1974) and Löfgren (1978) assigned the latter species to the genus *Cornuodus*.

Some elements assigned to *Protopanderodus reclinatus* (Lindström) s.l. are probably conspecific with, or part of a species closely related to, *P.* n. sp. A. Other elements of *P. reclinatus* are herein reassigned to other species of *Protopanderodus* (see *P.* n. sp. A).

The lower Llanvirn Protopanderodus sp. A Stouge does not contain symmetrical acontiodontiform (*c*) elements. Its asymmetrical acontiodontiform (*a/b*) elements have a costa on one face and a sharp-edged groove on the other. Stouge (1984) thought that this species alternatively could be a juvenile form of *P. strigatus* Barnes and Poplawski, which occurs in the same strata. Stouge's second interpretation is favoured in the present study.

Protopanderodus sp. from the McLish Formation, Oklahoma (Dzik, 1983, Fig. 3:30), has two types of elements. One has a groove (possibly bounded by costae) on one face and an unornamented opposite face. Only one face is illustrated on the other element; this face has one costa. This species occurs within the *Pygodus serra* to *Pygodus anserinus* zones (Sweet and Bergström, 1976, p. 147).

Other species excluded from the present report are not well known, informally named (in the sense of single element taxonomy), or only questionably assigned to *Protopanderodus*.

PROTOPANDERODUS EVOLUTIONARY EVENTS

Six notable events in the evolution of *Protopanderodus* are: 1) the transition from *Drepanodus* to an ancestral bicostate species of *Protopanderodus* by or before the early Arenig; 2) the origin of the multicostate lineage by the middle Arenig; 3) the existence of a possible Pacific fauna comprising two lower to middle Arenig bicostate species and two multicostate middle Arenig species; 4) the divergence of both lineages in the late Arenig to early Llanvirn; 5) the termination of the bicostate lineage in the early Caradoc; 6) the evolution of *P. insculptus* from *P. liripipus* by the early Ashgill. It is possible to link some of these events to times of global sea-level changes (Fig. 2), and other faunal events.

The following discussion makes reference to: a) paleogeographic occurrences – i.e., the Iapetus Ocean, and cratonic and marginal seas of Baltica, China, Gondwana and Laurentia (for brevity, these cratonic seas simply will be identified by the name of the adjacent continental mass); and b) provinciality – i.e., North American Midcontinent and North Atlantic conodont faunal provinces.

Fortey (1984) suggested that during regression, shallow oceanic environments expanded, and may have provided sites of retreat for shelf species. New species originating in oceanic areas could potentially contribute to cratonic faunas in subsequent transgressions. Therefore, an Iapetus-based distribution of *Protopanderodus* (or one that is at least marginal or extra-cratonic), combined with eustatic changes, may have significance for the major events noted in the evolution of the genus.

Dzik (1983, Fig. 12) calculated index of diversity values for Ordovician conodont species – the smaller the value, the more dominant the species. These values do not always correspond to the relative abundance patterns of Dzik (1983, Fig. 11), which are based on conodont families. Dzik (*ibid.*, p. 83) stated that a significant decrease in species diversity is usually connected with shallowing of basins. However, when compared to major eustatic changes, there are exceptions to this pattern.

Events 1 and 2

Bicostate *Protopanderodus* had appeared by the early Arenig or possibly late Tremadoc, the multicostate forms by the middle Arenig (Fig. 2). Barnes (1984) recognized a regressive phase in strata of the Canadian part of Laurentia that is uppermost Tremadoc to lowermost Arenig (*Paroistodus proteus* to *Prioniodus elegans* zones), and which was preceded and followed by transgressive phases in the Tremadoc (*Paltodus deltifer* and older zones), and middle Arenig (uppermost *P. elegans* to *Oepikodus smithensis* zones), respectively. The middle Arenig transgression on Laurentia was followed by a (short?) regressive interval approximately equal to the *Prioniodus* (*Baltoniodus*) *triangularis* Zone (Barnes, 1984) and then an uppermost Arenig transgression. Fortey (1984) also noted a global Tremadoc transgression, regression at the Tremadoc – Arenig boundary, and subsequent Arenig transgression (the last transgression corresponding to the short upper Arenig regression – transgression of Barnes, 1984). Evidence for this included the occurrence of shallow water platform carbonates and the sudden appearance of oceanic species.

The oldest bicostate species of *Protopanderodus* may be *P. elongatus* sensu Repetski (1982), and if so, it was present during the last phase of the late Tremadoc transgression. If, however, the lower limit of this species is that suggested by Serpagli (1974), then its appearance was instead coincident with the middle Arenig transgression.

Figure 2 appears to illustrate a diversification of *Protopanderodus* at the base of the Arenig *O. smithensis* Zone and therefore coincident with the middle Arenig transgression of Barnes (1984). However, the lineages of the bicostate species do not reflect speciation – they illustrate the subsequent appearances of *P. elongatus* and *P. rectus* at new localities. The oldest multicostate species are *P. gradatus* sensu Serpagli (1974) and *P. variabilis* of Gastil and Miller (1981) (see Figure 2). The appearances of these species correspond to the middle Arenig transgression.

It is tempting to suggest a relationship between the first appearances of both bicostate and multicostate species of *Protopanderodus* and the late Tremadoc and middle Arenig (respectively) transgressions. However, a more accurate means of determining the species first appearances must be implemented before a causal connection to eustatic events can be made (see also Event 3 below).

Event 3

Protopanderodus elongatus and *P. leonardii* are species from west-central Argentina (Gondwana) and the western Texas and Ibex, Utah areas (Laurentia). In Argentina, these species are from the middle Arenig (*O. smithensis* Zone), although *P. leonardii* seems to have a slightly lower range limit, whereas in Texas, they both may be as old as early Arenig (*P. elongatus* may be as old as late Tremadoc). The multicostate species *P. gradatus* sensu Repetski (1982) and Ethington and Clark (1982) (from Texas and Utah, respectively), and *P. varicostatus* sensu Gastil and Miller (northwestern Mexico), are both present in the middle Arenig *O. smithensis* Zone (Fig. 2). *Protopanderodus gradatus* is also reported from northeastern Arkansas (with *P. leonardii*; Ethington and Repetski, 1986), and from southern Oklahoma and western Alberta (Ethington and Clark, 1982, p. 84). These species originated sometime during the transgressive – regressive – transgressive cycle of the late Tremadoc – middle Arenig (see Events 1 and 2).

The paleogeographic position of Argentina, and western Mexico, United States and Canada suggests that the four species may be part of a Pacific-centred fauna. If the Texan forms of *Protopanderodus elongatus* and *P. leonardii* are indeed older than those from Argentina, they may be precocious species (sensu Fortey, 1984) that migrated during the early Arenig transgression. The appearances of these species, and the lower to middle Arenig *P.* cf. *P. rectus* in Texas and the middle Arenig *P. gradatus* s.l. and *P. varicostatus* s.l. in Texas and Mexico, respectively, may slightly predate occurrences of *P. rectus* and *P.* cf. *P. varicostatus* in Baltica and *P. gradatus* in the eastern Iapetus. If so, these suggest a western source of early bicostate and multicostate species, possibly from the western Iapetus or Pacific oceans.

Event 4

The diversification of both the bicostate and (to a lesser extent) multicostate groups of *Protopanderodus* coincides with a late Arenig regressive maximum and early Llanvirn transgression that were documented by Fortey (1984). On the Canadian part of Laurentia, data indicate a change in sea level from a transgressive phase in the late Arenig (*Prioniodus* (*Baltoniodus*) *navis* to *Microzarkodina flabellum parva* zones) to a regressive phase in the latest Arenig to earliest Llanvirn (*Amorphognathus variabilis* to lower *Eoplacognathus suecicus* zones), followed by a return to a transgressive phase within the upper part of the *E. suecicus* Zone (Barnes, 1984). (Lindström, 1984a, stated that this regressive phase corresponds to the slightly older *M. f. parva* to lower *A. variabilis* zones). The regression appears to have been accompanied by an early Llanvirn cooling event (Spjeldnaes, 1961; Webby, 1984), both of which may have been glacially controlled (Fortey, 1984; Lindström, 1984b).

Lindström (1984a) observed a relative scarcity, and even absence in some cases, of *Protopanderodus* in the lower *A. variabilis* Zone in many Baltoscandian sections. Because of the reverse distributional relationship between this genus and *Drepanoistodus*, Lindström thought that *Protopanderodus* could have preferred somewhat deeper water, but that both genera possibly had centres of distribution at or near the shelf.

At the beginning of the upper Arenig to lower Llanvirn *A. variabilis* Zone, there is a decrease in species diversity in conodont faunas from Baltica (Jämtland, Sweden; Dzik, 1983, Fig. 12E). Faunal diversity subsequently increases in the higher strata of this zone, reflecting the appearance of more species during the later phase of the early Llanvirn regression.

Event 5

Significant changes in the evolutionary lineages of *Protopanderodus* and other genera occur in the subzones of the Caradoc *Amorphognathus tvaerensis* Zone. There is a notable influx of species from the North American Midcontinent Province into the North Atlantic Province in the lower part of this zone (Sweet and Bergström, 1974).

In the *Prioniodus* (*Baltoniodus*) *variabilis* Subzone are the last known occurrences of *Protopanderodus graeai* and *P. rectus*? (both in New Brunswick) and the North Atlantic Province genera *Cahabagnathus* and *Complexodus* (Bergström, 1983). The bicostate lineage and the

multicostate species *Protopanderodus varicostatus* are not known above the higher *Prioniodus* (*Baltoniodus*) *gerdae* Subzone. *Protopanderodus robustus* from southern Tasmania and *P. varicostatus* from New Brunswick (Gondwana and Iapetus, respectively), and the North Atlantic Province species, *Pygodus anserinus* Lamont and Lindström, became extinct within the *P.* (*B.*) *gerdae* Subzone. New genera occur in this subzone, including *Rhodesognathus* (a cosmopolitan genus), and in the North American Midcontinent Province *Polyplacognathus* and *Scyphiodus* (Bergström, 1983).

In the strata of Iapetus (Holy Cross Mountains, Poland; Dzik, 1983, Fig. 12D) and Laurentia (Ardmore, Oklahoma; *ibid.*, Fig. 12B) diversity generally decreases in the *Amorphognathus superbus* Zone. Although Dzik (1983) related decreases in diversity to shallowing events, these reductions (and other changes noted above) correspond to the extensive Caradoc transgression (Lenz, 1982; Fortey, 1984), which continued possibly until the middle to late Ashgill (Brenchley and Newall, 1984).

Event 6

In the late Caradoc or early Ashgill, *Protopanderodus insculptus* evolved from *P. liripipus*. Distributions of these two species are not entirely equal – both are found in strata of central Queensland, southern Tasmania and the Carnic Alps (Gondwana), eastern Yangtze gorges (China), and North America (Laurentia, Iapetus), but only *P. liripipus* is known from Wales and southern Norway (Baltica). The movement of Baltica, which reached low latitudes by the middle or late Ashgill (Webby, 1984), and the final Ordovician eustatic regression probably complicate evolutionary and ecological patterns.

The Late Ordovician glacio-eustatic regression coincided with the demise of many species and genera, including *Protopanderodus* (see Sweet and Bergström, 1984 for a discussion on Late Ordovician conodont provincialism and extinction).

SYSTEMATIC PALEONTOLOGY

Remarks. Conodont Colour Alteration Index (CAI) values of Ordovician elements from northern Yukon (which include elements of other genera as well as *Protopanderodus*) are as follows: Blackstone River, 4; upper Peel River, 4; Rock River, 4.5 to 5; Tetlit Creek, 4.5.

Some of the material housed in the National Type Fossil Collection at the Geological Survey of Canada (GSC) in Ottawa were studied for this report. These are denoted below in the synonymies by a "v" for *vidimus*; "vv" indicates that elements from the same sample as the type specimens were studied in addition to the types. All illustrated elements are assigned GSC type numbers and are housed in the National Type Fossil Collection in Ottawa. Taxon names are multielement, unless qualified by the abbreviation "s.f." or listed as discrete elements in the synonymy lists. The element nomenclature is from Barnes et al. (1979).

Class CONODONTATA Pander, 1856

(*nom. transl.* Fåhraeus, 1983, *ex* Conodonta)

Order CONODONTOPHORIDA Eichenberg, 1930

Superfamily DISTACODONTACEA Bassler, 1925

(*nom. correct.* Hass, 1958, *pro* Distacodidae; *nom. transl.* Lindstrom, 1970, *ex* Distacodontidae)

Family PROTOPANDERODONTIDAE Lindström, 1970

(*nom. transl.* Bergström in Robison, 1981, *ex* Protopanderodontinae)

Subfamily PROTOPANDERODONTINAE Lindstrom, 1970

Remarks. The suprageneric interpretation of *Protopanderodus* and its relationship to other genera have undergone some changes since Lindström (1970, 1971) indicated that *Protopanderodus* (Superfamily Panderodontacea Lindström) was probably more closely allied to *Panderodus*, and *Drepanodus* (Superfamily Distacodontacea Bassler) was more closely allied to *Drepanoistodus*, *Paltodus*, and *Paroistodus*, than to each other (e.g., Dzik, 1976, 1983; Löfgren, 1978; Fåhraeus and Hunter, 1985, 1986).

Bergström (in Robison, 1981) revised the suprageneric classification with both *Protopanderodus* and *Drepanodus* being within the Family Protopanderodontidae, which includes genera with, and without, a costae-symmetry transition series (the family does not include *Drepanoistodus*, or *Paroistodus*, which are part of the Family Drepanoistodontidae Bergström, or *Paltodus*, which is classified as Family Unknown). Both Drepanoistodontidae and Protopanderodontidae of Bergström (*ibid.*) belong under the Superfamily Distacodontacea, which excludes *Panderodus*.

Stouge (1984) had a similar interpretation, with Drepanodus being part of the Subfamily Protopanderodontinae Lindström along with *Protopanderodus* and his new genus *Parapaltodus*. In Stouge's view, the Subfamily Drepanoistodontinae Fåhraeus and Nowlan encompasses *Drepanoistodus*, *Paltodus* and *Paroistodus*. He placed the distinction between *Protopanderodus* and *Panderodus* at the family level.

The writer of the present report concurs with the interpretation of Löfgren (1978), Bergström (in Robison, 1981), Dzik (1983) and Stouge (1984) that the relationship between *Protopanderodus* and *Panderodus* is distant.

The characteristic feature of *Protopanderodus* is the symmetry series comprising *a/b-c* elements and is based on the variable presence and position of lateral costae and torsion of the element. This symmetry series has been noted previously (e.g., Serpagli, 1974; Löfgren, 1978). A secondary symmetry character is that seen in the curvature of the cusp. The costae-symmetry series is rare or absent in *Drepanodus*. The apparatus of the type species *Drepanodus arcuatus* Pander is based on the degree of cusp inclination and torsion (i.e. a form of symmetry variation); the apparatus comprises *a/b-c* and *e* (drepanodontiform and scandodontiform, respectively) elements. Stouge (1984, p. 46) also recognized both a curvature transition series and a symmetry transition series in *Drepanodus*; the latter series is characterized by the twisted nature of the cusp (i.e., the torsion-symmetry character as mentioned above).

The following suprageneric classification is herein proposed: Superfamily Distacodontacea, Family Protopanderodontidae, Subfamily Protopanderodontinae – comprising variably twisted (torsion-symmetry) unicostate to multicostate *a/b-c* (acontiodontiform) elements within a costae-symmetry and cusp-curvature transition series, and acostate, carinate or costate *e* (scandodontiform) elements,

and consisting of *Protopanderodus*; Subfamily Drepanodontinae Fåhraeus and Nowlan – comprising a cusp-curvature transition series of variably twisted acostate to rarely costate *a/b-c* (drepanodontiform), and acostate *e* (scandodontiform) elements and consisting of *Drepanodus*, *Parapaltodus*; Family Drepanoistodontidae, Subfamily Drepanoistodontinae Fåhraeus and Nowlan (*nom. correct.* Stouge, *pro* Drepanoistodinae) – comprising a cusp-curvature transition series of variably twisted *a/b-c* (one to two distinct drepanodontiform) elements, and a geniculate *e* (oistodontiform) element (all can vary from acostate to costate) and consisting of *Drepanoistodus*, *Paltodus*, *Paroistodus*, and possibly *Besselodus*.

Genus *Protopanderodus* Lindström, 1971 emend. herein

Type species. *Acontiodus rectus* Lindström, 1955.

Diagnosis. *Protopanderodus* comprises elements of a costae-symmetry transition series (acontiodontiform or *a/b*, *c* elements), and a scandodontiform (*e*) element. The acontiodontiform elements vary in symmetry due to position and/or number of lateral costae. The *a/b* element is asymmetrical; the *c* element is symmetrical, or nearly so. Elements have a cusp that is higher than the base; acontiodontiform elements may vary in cusp recurvature and have a secondary, torsion-symmetry character. Large asymmetrical acontiodontiform (gigantiform) elements are multicostate with very short bases; these may be gerontic elements. Some acontiodontiform elements in one species, *P. insculptus* (Branson and Mehl), have a single denticle on the posterior part of the base; these elements also vary in the degree of symmetry.

Remarks. Lindström (1971), in his original diagnosis of *Protopanderodus*, and Stouge (1984), in a subsequent emendation, included the fact that longitudinal striations on the cusp may be inconspicuous. Löfgren (1978) illustrated this microstructure, and noted that in a few elements these striae are assembled into bundles anterior to the lateral costae. The present emended diagnosis omits reference to microstructure, partly because this type of ornamentation can be found in other genera, but primarily because it may be inconspicuous, and thus seen only on well preserved specimens.

In most cases, the acontiodontiform elements are readily differentiated into asymmetrical (*a/b*) and symmetrical (*c*) elements. It is questionable whether the *a/b* elements can be further divided into distinct *a* and *b* elements (see Evolution of *Protopanderodus* section, above).

Almost all species of *Protopanderodus* include *c* elements. Even *P. gradatus* Serpagli could be considered similar in this regard; it comprises a transition series from asymmetrical to nearly symmetrical elements (cf. Serpagli, 1974, p. 75, Fig. 17). Repetski (1982) offered a different view and suggested that his acostate element of *P.* cf. *P. gradatus* could be the symmetrical element of *P. gradatus*. *Protopanderodus* cf. *P. varicostatus* (Sweet and Bergström) sensu Löfgren (1978) differs from other species in that practically all acontiodontiform elements are asymmetrical with two costae on one side and one on the other. In this regard the species is markedly different from other species of *Protopanderodus*. Löfgren (1978, p. 92), however, was cautious in not excluding the possibility of incorrect assignment of symmetrical elements to other species. Stouge (1984) equated his *P.* cf. *P. varicostatus* with Löfgren's species, and included symmetrical acontiodontiform elements similar to *Acontiodus cooperi* Sweet and Bergström s.f., which he considered as part of *P. varicostatus*. *Acontiodus cooperi* s.f. is included tentatively herein as a *c* element of *P. robustus*.

Scandodontiform elements (excluding that mentioned below as a possible *a* element in *Protopanderodus* n. sp. A) have a cusp that is more laterally twisted compared with the acontiodontiform elements. From this, and the ornamentation, it would appear that the scandodontiform elements are not part of the first symmetry transition series, but rather part of the second (i.e., the *e* element).

Gigantiform elements similar in form to *Scolopodus giganteus* Sweet and Bergström s.f., are long ranging and may be part of different species of *Protopanderodus* (cf. *P. insculptus*, *P. liripipus* Kennedy et al., *P. varicostatus* (Sweet and Bergström) s.s., *P.* cf. *P. varicostatus*, herein). The position of gigantiform elements within an apparatus is not clear, but Landing (1976, p. 640) suggested that *S. giganteus* s.f. may be a "senile" variant of his *Acontiodus robustus* s.f. (*P. robustus*, herein). Other gigantiform elements may be part of the multielement *Scolopodus*.

The posteriorly denticulated acontiodontiform elements in *Protopanderodus insculptus* show some variation in symmetry and are regarded as rare varieties of the *a/b* and *c* elements.

Protopanderodus insculptus (Branson and Mehl)

Plate 3, figures 9-14, 17, 19,
Figure 3K-P

a/b-c elements

Phragmodus insculptus BRANSON and MEHL, 1933, p. 124, Pl. 10, figs. 32-34 (fig. 32 = denticulate element).

?*Protopanderodus insculptus* (Branson and Mehl) s.f. PALMIERI, 1978 (in part), p. 25, Pl. 2, figs. 28, 29 only [figs. 26, 27, Fig. 4(10a-c) = *P. liripipus* Kennedy et al., below].

Protopanderodus insculptus (Branson and Mehl) s.f. ROSS, NOLAN, and HARRIS, 1980, Fig. 6a-c.

Scolopodus insculptus (Branson and Mehl). BERGSTRÖM and SWEET, 1966, p. 398-400, Pl. 34, figs. 26, 27, Fig. 13B (includes synonymy); v ?GLOBENSKY and JAUFFRED, 1971, p. 58, Pl. 5, fig. 10 (quadricostate *a/b* element; large gerontic or pathological form); ?VIIRA, 1974, Pl. 13, fig. 8 (anterolateral corner broken); ?MILLER, 1976, Fig. 8(53).

Scolopodus? *insculptus* (Branson and Mehl). SERPAGLI, 1967 (in part), p. 97-99, Pl. 28, fig. 2a, b (other elements are equated herein with *P. liripipus* Kennedy et al., and possibly with *P.* sp. B).

non *Scolopodus insculptus* (Branson and Mehl). HAMAR, 1966, p. 75, 76, Pl. 1, fig. 18, Fig. 2(1) [= *P. varicostatus* (Sweet and Bergström) by Kennedy et al., 1979].

e element

Phragmodus dissimilaris BRANSON and MEHL, 1933, p. 123, 124, Pl. 10, fig. 29.

Scandodus dissimilaris (Branson and Mehl). SERPAGLI, 1967, p. 94, 95, Pl. 24, figs. 5a-6c.

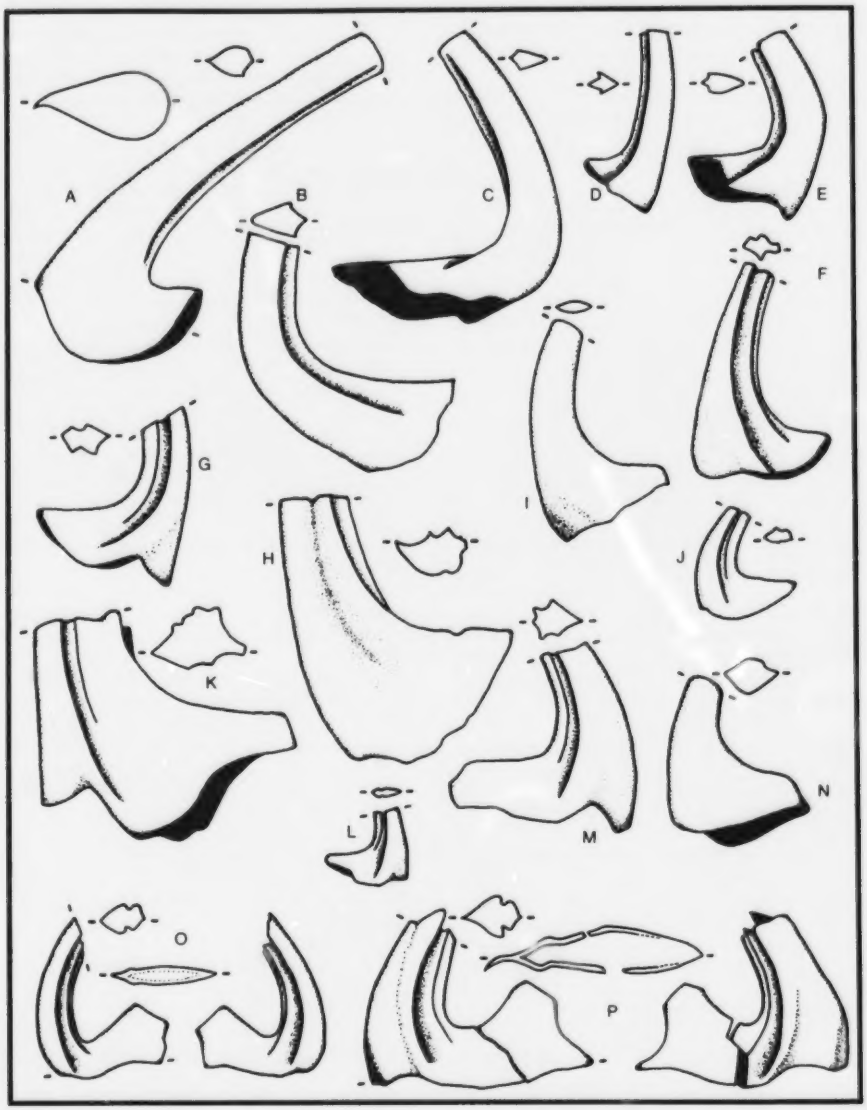


Figure 3. *Camera-lucida drawings of lateral faces and cross-sections of* **Protopanderodus** *species from northern Yukon. Lower side of all cross-sections is the lateral face shown in this figure. Figures A-N are approximately x57; cusp cross-section of figure O is x57; figure P, and base cross-section and lateral view of figure O are x28. All elements except those of figure O (GSC 69198) and P (GSC 82837) are illustrated in Plates 1 and 2.*

A-C. **Protopanderodus** *n. sp. A. (A) – a/b element, lateral view shows costate outer face (GSC 82869; Pl. 1, fig. 18); (B) – c element (GSC 82865; Pl. 1, fig. 13); (C) – c element (GSC 82864; Pl. 1, fig. 12).*

D. **Protopanderodus parvibasis** *Löfgren. c element (GSC 82848; Pl. 1, fig. 26).*

E. **Protopanderodus robustus** *(Hadding). Short-based c element (GSC 82850; Pl. 1, fig. 1).*

F. **Protopanderodus** *cf. P.* **varicostatus** *(Sweet and Bergström). a/b element (GSC 82859; Pl. 3, fig. 3).*

G-J. **Protopanderodus liripipus** *Kennedy, Barnes and Uyeno. (G) – c element (GSC 82842; Pl. 3, fig. 21); (H) – gigantiform element, outer lateral view (GSC 82839; Pl. 3, fig. 16); (I) – e element, outer lateral view (GSC 82846; Pl. 3, fig. 25); (J) – a/b element (GSC 82845; Pl. 3, fig. 24).*

K-P. **Protopanderodus insculptus** *(Branson and Mehl). (K) – gigantiform element (GSC 82834; Pl. 3, fig. 14); (L) – c element (GSC 82831; Pl. 3, fig. 11); (M) – a/b element (GSC 82832; Pl. 3, fig. 12); (N) – e element, outer lateral view (GSC 82836; Pl. 3, fig. 19); (O) – denticulate c element (GSC 69198 from Lenz and McCracken, 1982); (P) – denticulate a/b element (GSC 82837; not figured in plates).*

Scandodus sp. cf. *S. dissimilaris* (Branson and Mehl). BERGSTRÖM and SWEET, 1966, p. 396, 397, Pl. 34, figs. 24, 25, ?Fig. 13D.

Multielement

Protopanderodus insculptus (Branson and Mehl). SWEET, THOMPSON, and SATTERFIELD, 1975, Pl. 1, figs. 19, 20 (fig. 19 = denticulate element); ?DZIK, 1976, Figs. 16h, k (tentative due to broken bases); HARRIS, BERGSTRÖM, ETHINGTON, and ROSS, 1979, Pl. 4, fig. 2 (denticulate element); AN, 1981, Pl. 3, fig. 28 (denticulate element); vv LENZ and McCRACKEN, 1982, Pl. 1, figs. 14-16, 21 (= *c*, denticulate, *c*, *a/b* elements; all are quadricostate); AN et al., 1985, Pl. 11, fig. 18 (denticulate element); CRAIG, 1986, Pl. 2, fig. 34 (denticulate element).

Protopanderodus? *insculptus* (Branson and Mehl). ZENG et al., 1983, Pl. 12, fig. 37 (denticulate element).

aff. *Protopanderodus* n. sp. aff. *P. insculptus* (Branson and Mehl). HARRIS, BERGSTRÖM, ETHINGTON, and ROSS, 1979, Pl. 5, fig. 4.

Remarks. Three modified acontiodontiform elements that have a posterior denticle are present in material from northern Yukon; a fragmentary element may also be one of these forms (see Evolution of *Protopanderodus*). The denticulate element shown by Lenz and McCracken (1982) is symmetrical – the paired costae are nearly directly opposed, and the element is not twisted. This is regarded as a variety of the *c* (symmetrical acontiodontiform) element (Fig. 3O). One of the denticulate elements (Fig. 3P) is asymmetrical in the sense that a lower anterior keel is deflected to the inner side; this is termed the *a/b* (asymmetrical acontiodontiform) element. The pair of costae on the inner side of this element are slightly anterior to the two costae on the opposite side. All denticulate elements from northern Yukon have sharp anterior and posterior margins; the latter are bounded by the posterolateral costae. These denticulate elements lack antero-aboral notches, but one is present in the specimens of Sweet et al. (1975) and Harris et al. (1979).

Only one denticulate element is fully preserved posterior to the denticle. In this element, the base posterior to the denticle is short and tapers to a point (Fig. 3P). The short length is similar to that shown in elements of *Protopanderodus insculptus* in An (1981) and Harris et al. (1979). This part of the base is relatively long in the element of the specimen in Sweet et al. (1975).

Nowlan (1976) illustrated a denticulate element of *Protopanderodus insculptus* from Fauna 11 (Edenian-Maysvillian) of Grinnell Peninsula, Devon Island, Northwest Territories. Other elements of his species should be assigned to *P. liripipus* Kennedy et al.

Most adenticulate *a/b* elements (Pl. 3, figs. 9, 10, 12, 17; Fig. 3M) are quadricostate, although some have only three costae. The *e* elements (Pl. 3, figs. 13, 19; Fig. 3N) have a keeled posterior oral margin, prominent inner lateral costae bounding a deep medial groove, and a narrowly convex outer cusp face, and thus differ from the same element of *Protopanderodus liripipus* Kennedy et al. (see below).

Scandodus dissimilaris s.f. of Serpagli (1967) is considered to be an *e* element of *Protopanderodus insculptus* because of the sharp costate edges bordering the groove on its inner face.

The gigantiform element (Pl. 3, fig. 14, Fig. 3K) is large and on one face has four costae, one of which bifurcates at the base, and on the other face has two costae. The base of the element is not laterally twisted.

Occurrences. The lower limit of *Protopanderodus insculptus* and its exact relationship to *P. liripipus* is not clear, but both species occur within the Ashgill. At Blackstone River, they occur in association with *Amorphognathus ordovicicus* Branson and Mehl, rare *Gamachignathus ensifer* McCracken et al. and rare *Noixodontus girardeauensis* (Satterfield). This fauna is from a level between beds of the *Paraorthograptus pacificus* Zone and the tentative *Glyptograptus persculptus* Zone. This occurrence indicates that both species range upward to the upper Ashgill *G. ensifer* Zone.

The occurrences of other species in the synonymy are: (listed in alphabetical order of authors) An, 1981, Middle Ordovician, Yunnan Province, southern China; An et al., 1985, *P. insculptus* Zone (Ashgill, upper *A. superbus* and *A. ordovicicus* zones), Hubei Province, China; Bergström and Sweet, 1966, Middle Ordovician, central United States; Branson and Mehl, 1933, Upper Ordovician, Missouri; Craig, 1986, Fauna 9 or 10 (pre-*A. ordovicicus* Zone), Fauna 11, Fauna 12 (*A. ordovicicus* Zone), northeastern Arkansas; Globensky and Jauffred, 1971, Middle Ordovician, southwestern Quebec; Harris et al., 1979, Faunas 11-12 (upper Edenian – Richmondian), *A. ordovicicus* Zone, Nevada; Lenz and McCracken, 1982, upper Ashgill, northern Yukon; Palmieri, 1978, Fauna 12 and *A. ordovicicus* Zone, central Queensland, Australia; Ross et al., 1980, Ashgill, central Nevada; Sweet et al., 1975, Richmondian, eastern Missouri; Serpagli, 1967, Ashgill, Carnic Alps; Viira, 1974, *A. triangularis frognoeyensis* Zone (Upper Ordovician), east Baltic; Zeng et al., 1983, *P.*? *insculptus* Zone (Ashgill) eastern Yangtze gorges, China (*P. insculptus* of Fig. 2).

Material. 4 denticulate, 13 *a/b*, 9 *c*, 2 *e*, 1 gigantiform elements.

Types. Hypotypes, GSC 69198, 82829-82837.

Protopanderodus liripipus Kennedy, Barnes, and Uyeno

Plate 3, figures 15, 16, 18, 20-25,
Figure 3G-J

a/b-c elements

?*Protopanderodus insculptus* (Branson and Mehl) s.f. PALMIERI, 1978 (in part), p. 25, Pl. 2, figs. 26, 27, Fig. 4(10a-c) only (Pl. 2, figs. 28, 29 = *P. insculptus*, above).

Scolopodus insculptus (Branson and Mehl). v WINDER, 1966, p. 60, 61, Pl. 9, fig. 21, Fig. 3(21) (quadricostate *a/b* element); VIIRA, 1974, Pl. 13, fig. 8.

Scolopodus? *insculptus* (Branson and Mehl). SERPAGLI, 1967 (in part), p. 97-99, Pl. 28, figs. 1a, b, 3a-4b (Pl. 28, figs. 2a, b = *P. insculptus*; Pl. 28, figs. 5a-6b = ?*P.* sp. B, herein).

e element

Acodus sp. cf. *A. dissimilaris* (Branson and Mehl). v WINDER, 1966, p. 51, 52, Pl. 9, fig. 3, Fig. 3(3).

Multielement

Protopanderodus insculptus (Branson and Mehl). ?DZIK, 1976, p. 443, Figs. 16h, k (broken bases); FLAJS and SCHÖNLAUB, 1976, Pl. 3, fig. 9; v BARNES, 1977, p. 108, Pl. 3, fig. 3.

?*Protopanderodus* cf. *P. insculptus* (Branson and Mehl). TIPNIS, CHATTERTON, and LUDVIGSEN, 1978, Pl. 9, fig. 6.

Protopanderodus liripipus KENNEDY, BARNES, and UYENO, 1979, p. 546-550, Pl. 1, figs. 9-19 (types viewed; includes synonymy); AN, 1981, Pl. 3, fig. 29; vv NOWLAN, 1981a, p. 14, Pl. 5, figs. 6-8 (quadricostate *a/b*, *e*, quadricostate *a/b* elements, respectively); WANG and WANG, 1981, Pl. 1, fig. 4; BURRETT, STAIT, and LAURIE, 1983, p. 184, Figs. 9A, B; WANG et al., 1983, p. 154, 155, Pl. 8, fig. 11; ZENG et al., 1983, Pl. 12, fig. 34; AN et al., 1985, Pl. 12, figs. 5-9; vv NOWLAN and McCRACKEN in NOWLAN, McCRACKEN, and CHATTERTON, 1988, Pl. 11, figs. 18, 20 (*c*, quadricostate *a/b* elements; includes synonymy); BERGSTRÖM in BERGSTRÖM and ORCHARD, 1985, Pl. 2.3, fig. 4; SAVAGE and BASSETT, 1985, Pl. 86, fig. 15.

Protopanderodus Liripipus (sic) Kennedy, Barnes, and Uyeno. AN, 1981, Pl. 3, fig. 29.

Protopanderodus cf. *P. liripipus* Kennedy, Barnes, and Uyeno. vv NOWLAN, 1981b, Pl. 3, fig. 23 (quadricostate *a/b* element); v NOWLAN, 1983, p. 667, Pl. 3, figs. 12, 15 (quadricostate *a/b* elements).

Protopanderodus cf. *liripipus* Kennedy, Barnes, and Uyeno. ?ORCHARD, 1980, p. 24, Pl. 4, figs. 27, 33; cf. STOUGE, 1984, p. 49, 50, Pl. 2, figs. 9-14, 17.

Scolopus (sic) *insculptus* (Branson and Mehl). v BARNES, 1974, Pl. 1, fig. 19 (quadricostate *a/b* element).

Remarks. An element equivalent to the uncommon denticulate element of *Protopanderodus insculptus* (Sweet and Bergström) is not recognized in the otherwise morphologically similar *P. liripipus*. This writer has viewed the *P. liripipus* material of Nowlan (1981a; GSC locality 96064), which is from near the locality reported in Kennedy et al. (1979). There are no denticulate forms (or broken denticles) among the 310 *a/b-c* elements, whereas four of 26 acontiodontiform elements of *P. insculptus* from northern Yukon are denticulate. This suggests that unlike *P. insculptus*, *P. liripipus* lacks a denticulate element.

The *a/b* elements of *Protopanderodus liripipus*, *P. insculptus* and *P. varicostatus* (Branson and Mehl) s.l. are quite similar, and incomplete specimens are indistinguishable. This similarity creates a problem due to the stratigraphic overlap of *P. liripipus* with the older *P. varicostatus* and the younger *P. insculptus*.

Most *a/b-c* elements of *Protopanderodus liripipus* are unkeeled, but one long-based *c* element (Pl. 3, fig. 23) has a low keel; however, this is not as well developed as that of *P. insculptus*. The antero-aboral notch on most *a/b-c* elements of *P. insculptus* is more developed compared with that in *P. liripipus*.

Almost all *a/b* elements in the northern Yukon collections are quadricostate, with weaker costae on one side. One element in the collection (Pl. 3, fig. 18) has a pair of costae on one lateral face, but seems to lack ornamentation on the other; another (Pl. 3, fig. 24; Fig. 3J) has three costae on one face and two on the other. The element of *Protopanderodus insculptus* figured by Barnes (1977), and unfigured elements of *P. liripipus* from Nowlan (1981a) have similar bicostate and acostate faces.

Protopanderodus cf. *P. varicostatus* (below) has some *a/b* elements (Pl. 3, fig. 3) that have bases like those found on some elements of *P. liripipus*. The antero-aboral notch on these elements of *P.* cf. *P. varicostatus* differs in that it is not strong.

The *e* elements of *Protopanderodus liripipus* and *P. insculptus* have the same outline but differ in the position of the groove on the inner lateral face. The groove on the *e* element of *P. liripipus* (Pl. 3, fig. 25; Fig. 3I) is near the anterior and is bounded by rounded margins. The groove on the *e* element of *P. insculptus* (Pl. 3, figs. 13, 19) is more medial and has sharp, costate edges. The depth of the groove on *e* elements in the sample from Nowlan's (1981a) GSC locality 96064 varies; the grooves on most are deeper than on elements from northern Yukon. A similar variation is shown in Kennedy et al. (1979, Pl. 1, figs. 18, 19). The *e* element figured herein also has a more compressed cusp compared with the *e* element of *P. insculptus*.

The lateral groove on the illustrated *e* element of *Protopanderodus* cf. *P. liripipus* of Stouge (1984, Pl. 2, fig. 17A) has a position more like that in *P. liripipus* (herein) than in *P. insculptus*, but the sharpness of the margins of the groove resemble the *e* element of *P. insculptus*. Stouge (1984) saw similarities between his scandodontiform element and that of Löfgren's *P.* cf. *P. varicostatus* (1978, Pl. 3, fig. 30; = *P.* cf. *P. varicostatus*, herein); it is also similar to the element of *P. liripipus* illustrated by Kennedy et al. (1979, Pl. 1, fig. 19). Kennedy et al. (1979) noted that the scandodontiform element lacks a rounded postero-aboral region on the base, a feature found on Löfgren's specimen – this could be a distinguishing characteristic for otherwise very similar elements of *P. liripipus* and *P.* cf. *P. varicostatus*.

The gigantiform element (Pl. 3, fig. 16; Fig. 3H) has a base that is noticeably twisted to one side; this inner side has three costae, the other has one costa and a shallow, medial groove.

Occurrences. Kennedy et al. (1979) suggested that the transition from *Protopanderodus varicostatus* (s.l.) to *P. liripipus* is in the *Prioniodus* (*Baltoniodus*) *gerdae* Subzone, with a slight overlap in their ranges, or possibly in the underlying *Pygodus anserinus* Zone, based on the work of Repetski and Ethington (1977). Two similar species that may extend the lower range of *P. liripipus* are *P.* cf. *P. insculptus* sensu Tipnis et al. (1978) and *P.* cf. *P. liripipus* of Stouge (1984). The former is associated with species of the *Pygodus serra* Zone in southwestern Northwest Territories; the latter occurs about the middle of the older *Amorphognathus variabilis – Microzarkodina ozarkodella* Subzone and ranges through most of the *Eoplacognathus suecicus – Panderodus sulcatus* Subzone of western Newfoundland.

Occurrences of other species listed in the synonymy are: (listed in alphabetical order of authors) An, 1981, Middle Ordovician, Anhui Province, southern China; An et al., 1985, *H. europaeus* Zone (*P. gerdae* to *A. superbus* zones) to *P. insculptus* Zone (*A. superbus* to *A. ordovicicus* zones) (Caradoc – Ashgill), Hubei Province, China (*P. liripipus* in Fig. 2); Barnes, 1974, Middle to Late Ordovician, Bathurst Island, Northwest Territories; Barnes, 1977, Edenian – Maysvillian, Melville Peninsula, N.W.T.; Bergström

and Orchard, 1985, *A. tvaerensis* Zone, southern Scotland; Burrett et al., 1983, upper *A. tvaerensis* Zone, southern Tasmania; Dzik, 1976, *A. superbus* Zone, Poland; Flajs and Schönlaub, 1976, Ashgill, Austria; Kennedy et al., 1979, *P.* (*B.*) *alobatus* Subzone, northern New Brunswick; Nowlan, 1981a, *P.* (*B.*) *alobatus* Subzone, northern New Brunswick (*P. liripipus* in Fig. 2); Nowlan, 1981b, Ashgill, Gaspésie, Quebec; Nowlan, 1983, *A. ordovicicus* Zone, northern New Brunswick; Nowlan et al., 1988, Richmondian Fauna 12, southwestern Northwest Territories; Orchard, 1980, *A. ordovicicus* Zone, Britain; Palmieri, 1978, late Middle to Late Ordovician, central Queensland, Australia; Savage and Bassett, 1986, *A. ordovicicus* Zone, Britain; Serpagli, 1967, Ashgill, Carnic Alps; Stouge, 1984, at one level within the middle *A. variabilis – M. ozarkodella* Subzone, and throughout the *E. suecicus* Zone, western Newfoundland (*P.* cf. *liripipus* in Fig. 2); Tipnis et al., 1978, upper Llanvirn, recorded as Llandeilo, but fauna of their locality 5 includes *Cahabagnathus friendsvillensis* (Bergström) and *Pygodus serra* (Hadding), Road River Formation, southwestern Northwest Territories; Viira, 1974, east Baltic; Wang et al., 1983, uppe *Dicellograptus szechuanensis* Zone (Ashgill), eastern Yangtze gorges, China; Winder, 1966, Middle Ordovician, southwestern Ontario; Zeng et al., 1983, *P.? insculptus* Zone (upper *A. superbus* and *A. ordovicicus* zones), eastern Yangtze gorges, China (*P. liripipus* in Fig. 2).

Material. 10 *a/b*, 5 *c*, 2 *e*, 1 gigantiform elements.

Types. Hypotypes, GSC 82838-82846.

Protopanderodus parvibasis Löfgren

Plate 1, figures 25, 26, 28, 29,
Figure 3D

Multielement

Protopanderodus parvibasis LÖFGREN, 1978, p. 93, Pl. 3, figs. 11-18, Fig. 31D-F.

Remarks. The two small *c* elements illustrated herein (Pl. 1, figs. 25, 26; Fig. 3D) have a short and low base. They differ from those of *Protopanderodus parvibasis* illustrated by Löfgren (1978) in that their cusps are erect rather than slightly recurved.

The single, laterally compressed *e* element (Pl. 1, figs. 28, 29) has a short base and a slight expansion of the basal cavity on the inner anterior side. The median carina and shallow groove on the cusp's inner face as described by Löfgren (1978) was not noted in this specimen.

Occurrences. Löfgren (1978) reported that *Protopanderodus parvibasis* occurs in lower Llanvirn (middle *Amorphognathus variabilis – Microzarkodina ozarkodella* to lower *Eoplacognathus suecicus – Panderodus sulcatus* subzones) in Sweden (*P. parvibasis* s.s. in Fig. 2). The elements from the *Pygodus serra* Zone of northern Yukon (*P. parvibasis* in Fig. 2) reflect the first reported occurrence of *P. parvibasis* outside Europe.

Material. 2 *c*, 1 *e* elements.

Types. Hypotypes, GSC 82847-82849.

Protopanderodus robustus (Hadding)

Plate 1, figures 1-10,
Figure 3E

non *Scandodus dubius* BRADSHAW, 1969, p. 1161, Pl. 134, figs. 19-21, Fig. 4G, H (questionably included by Löfgren, 1978; may = *a*? element of *P.* n. sp. A, herein).

***a/b* element**

?*Acontiodus reclinatus* Lindström. BRADSHAW, 1969, p. 1148, Pl. 131, figs. 6, 9.

Acontiodus robustus (Hadding). SWEET and BERGSTRÖM, 1962, p. 1222, Pl. 169, fig. 11, Fig. 1 I; v UYENO and BARNES, 1970, p. 104, Pl. 21, figs. 18, 19, Fig. 7G (secondary costae on unfigured face, which shows a well developed antero-aboral notch); LANDING, 1976, p. 629, 630, Pl. 1, fig. 8.

?*Acontiodus robustus* (Hadding) sensu Sweet and Bergström. REPETSKI and ETHINGTON, 1977, Pl. 1, fig. 5.

non *Acontiodus robustus* (Hadding). BRADSHAW, 1969 (in part), p. 1148, Pl. 131, fig. 13 only (= ?gerontic *a/b* element; figs. 8, 10, 14 = *c* element of *P.* n. sp. A, herein; all figured elements assigned to *P. robustus* by Löfgren, 1978); v BARNES and POPLAWSKI, 1973, p. 768, 769, Pl. 2, fig. 15 (included by Lofgren, 1978; see *P.* n. sp. A, herein); NASEDKINA, 1975, Pl. 3, figs. 1, 2 [multicostate elements; = ?*P. varicostatus* (Sweet and Bergström) s.l., or ?*Scolopodus* sp., herein].

Acontiodus sp. NASEDKINA, 1975, Pl. 3, fig. 9.

Drepanodus robustus HADDING, 1913, p. 31, Pl. 1, fig. 5.

c element

?*Acontiodus cooperi* SWEET and BERGSTRÖM, 1962, p. 1221, 1222, Pl. 168, figs. 2, 3, Fig. 1G; BRADSHAW, 1969, p. 1147, Pl. 131, fig. 5; REPETSKI and ETHINGTON, 1977, Pl. 1, fig. 10; BURRETT, STAIT, and LAURIE, 1983, p. 180, Fig. 9E.

e element

Scandodus sp. SWEET and BERGSTRÖM, 1962, p. 1246, Pl. 168, figs. 13, 16.

Multielement

Protopanderodus cooperi (Sweet and Bergström). v ?BARNES and POPLAWSKI, 1973 (in part), p. 782, Pl. 4, fig. 15, unfigured hypotype GSC 30298 only [= *c* elements; for other elements see *P.* cf. *P. varicostatus* (Sweet and Bergström), *P.* n. sp. A, herein].

non *Protopanderodus cooperi* (Sweet and Bergström). LANDING, 1976, p. 638, 639, Pl. 4, figs. 6, 7 (fig. 6 = *a/b* element, possibly of *P. gradatus* Serpagli, *P. strigatus* Barnes and Poplawski or *P. varicostatus*; Fig. 7 = *a/b* element of *P.* n. sp. A, herein).

Protopanderodus robustus (Hadding). LÖFGREN, 1978, p. 94, 95, Pl. 3, figs. 32-35, Figs. 31G-J (includes synonymy); vv NOWLAN and THURLOW, 1984, p. 293, Pl. 2, figs. 7, 13, 14 (*a/b*, *c*, *e* elements); STOUGE, 1984 (in part), p. 49, Pl. 2, figs. 5-8 only (Pl. 2, figs. 3, 4 are tentatively included herein under *P.* n. sp. A).

non *Protopanderodus robustus* (Hadding). AN et al., 1983, p. 132, Pl. 15, fig. 21 (tentatively included herein under *P.* n. sp. A); AN et al., 1985, Pl. 11, figs. 15, 16 (tentatively included herein under *P.* n. sp. A).

Remarks. The base of the *a/b* element (Pl. 1, figs. 2, 4) is not laterally compressed and the cusp is relatively broad. An assignment of these elements to *Protopanderodus robustus* is based on the presence of these features. The lateral costa on each face of the *a/b* element is more medial than that of the *c* element, especially on the cusp. The inner face has a narrow carina that is strongest in the proximal region of the cusp and base. *Protopanderodus robustus* sensu Löfgren (1978, Fig. 31J) has an *a/b* element with a base that is rectangular in profile and has a straight aboral margin. Other elements of *P. robustus* in Löfgren (*ibid.*, Pl. 3, figs. 32, 33) and the *a/b* elements of *P. robustus* from northern Yukon have a convex aboral margin and a slight antero-aboral notch. Many of Löfgren's (1978, p. 94) *c* elements of *P. robustus* have an antero-aboral notch but others do not (*ibid.*, Fig. 31G); all *c* elements from northern Yukon have a notch. Since this notch can be variably developed on *a/b-c* elements of *P. robustus*, but seems to be poorly developed on elements of *P. parvibasis* Löfgren, it may be a distinguishing character when present. Löfgren's figured element (*loc. cit.*) is similar to elements placed herein with *P.* n. sp. A, except that the costae extend to the aboral margin.

An association of *Acontiodus cooperi* Sweet and Bergström s.f., *A. robustus* s.f. and *Scolopodus varicostatus* Sweet and Bergström s.f. is found in the studies by Sweet and Bergström (1962), Bradshaw (1969), Landing (1976), Repetski and Ethington (1977), Stouge (1984) and herein. Stouge (1984) tentatively regarded *A. cooperi* s.f. as a junior subjective synonym. His interpretation is essentially the same as those of Barnes and Poplawski (1973) and Landing (1976) for *Protopanderodus cooperi*. Barnes and Poplawski placed a conferred assignment on *S. varicostatus* s.f. in their synonymy of *P. cooperi*. Landing (1976) identified *P. cooperi* on the basis of the scandodontiform element. No symmetrical (i.e., *c*) elements were noted for his species but four asymmetrically costate elements were compared to *S. varicostatus* s.f.

Evidence for including *Acontiodus cooperi* s.f. under *Protopanderodus varicostatus* is not convincing, and the similarities of this form species with the *c* element of *P. rectus* suggest instead that *Acontiodus cooperi* s.f. be tentatively included within the synonymy of *P. robustus* as the *c* element. *Acontiodus cooperi* s.f. is further queried in the above synonymy because the elements figured in the studies of Sweet and Bergström (1962) and Burrett et al. (1983) have a convex rather than straight lower anterior margin, as in the elements from northern Yukon. Löfgren (1978, p. 94) recognized the similarity between the symmetrical elements of *P. robustus* and *A. cooperi* Sweet and Bergström s.f. but noted that the posterior keel of *A. cooperi* s.f. is fluted.

The *c* elements of both *Protopanderodus rectus* (Lindström) and *P. robustus* have a strong lateral costa on each face extending from the tip of the cusp to the basal margin. The *c* element of *P. robustus* differs from that of *P. rectus* in that it has a slightly longer base and a cusp that is slightly more recurved. Also, in long-based elements (Pl. 1, fig. 6), the anterior margin from the antero-aboral corner to the level of recurvature is longer and straighter than in the equivalent element of *P. rectus*. Other elements (Pl. 1, fig. 1; Fig. 3E) have a shorter base but maintain a straight anterior margin. The *c* elements of *P. rectus* illustrated by Löfgren (1978, Pl. 3, figs. 1-3) have a more evenly convex margin. The two *c* elements that Barnes and Poplawski (1973) assigned to *P. cooperi* are similar to the *c* elements of *P. robustus* sensu this study and of *P. rectus*. They have a relatively short base and thus are more like the *c* element of *P. rectus*.

The *c* element is distinguished from the same element of *Protopanderodus parvibasis* in being less laterally compressed, more recurved, and having a longer oral margin (Löfgren, 1978, p. 94).

The *e* element (Pl. 1, figs. 3, 5, 7-10) has a smooth to carinate inner face and a base that varies in height, but is distinguishable from the homologous short-based element of *Protopanderodus parvibasis*. The *e* element of *P. robustus* differs from the same element of *P. rectus* in being less twisted and by having a basal cavity that is laterally less expanded (Löfgren, 1978, p. 94). Löfgren regarded *Scandodus dubius* Bradshaw s.f. as a scandodontiform element of *P. robustus*. It has a similar outline, but it is preferable to assign it to *P.* n. sp. A.

Löfgren (1978, p. 52) suggested that *Acontiodus robustus* s.f. of Landing (1976) is part of his *Drepanodus arcuatus* Pander. Landing's *D. arcuatus* and *A. robustus* s.f. are herein equated with *Protopanderodus* n. sp. A and *P. robustus*, respectively. *Acontiodus robustus* s.f. sensu Landing (*ibid.*) is included within *P. robustus* because its lateral costa is basally strong compared with the weak costae on the *c* elements of *P.* n. sp. A. It should be noted, however, that the one element of Landing (1976) lacks surface microstructure; this is contrary to the original generic definition of *Protopanderodus*, but not to the present emendation (see above). *Acontiodus robustus* s.f. of Bradshaw (1969) was included under *P. robustus* by Löfgren (1978). All of the illustrated elements of Bradshaw's *A. robustus* s.f. have basally weak costae, and thus are also regarded as part of *P.* n. sp. A.

Occurrences. Löfgren (1978) found *Protopanderodus robustus* (Hadding) in the lower part of the *Eoplacognathus suecicus – Scalpellodus gracilis* Subzone (Llanvirn), and higher strata, of Sweden. She reported that its range could extend to the upper Llandeilo, and possibly into the Caradoc (*P. robustus* in Fig. 2). *Acontiodus cooperi* Sweet and Bergström s.f. and *Scandodus* sp. Sweet and Bergström s.f. were defined from upper Llandeilo strata in Alabama. *Protopanderodus cooperi* sensu Barnes and Poplawski (1973) is from the lower Llanvirn of southwestern Quebec. *Protopanderodus robustus* of Stouge (1984) is primarily from the *E. suecicus* Zone of western Newfoundland but is also found at one level in the older *Amorphognathus variabilis – Microzarkodina ozarkodella* Subzone.

The occurrences of other species in the synonymy are (listed in alphabetical order of authors): Bradshaw, 1969, Middle Ordovician, western Texas; Burrett et al., 1983, ?*P.* (*B.*) *gerdae* Subzone, southern Tasmania (Fig. 2); Landing, 1976, *Paraglossograptus tentaculatus* Zone (?lower Llanvirn), eastern New York; Nasedkina, 1975, Arenig (occurs with *Spinodus spinatus* (Hadding), lower Whiterock Series), southern Urals; Nowlan and Thurlow, 1984, lower Whiterock

(uppermost Arenig – lower Llanvirn), central Newfoundland (Fig. 2); Repetski and Ethington, 1977, *P. anserinus* Zone, Arkansas, Oklahoma.

Material. 15 *a/b*, 10 *c*, 7 *e* elements.

Types. Hypotypes, GSC 82850-82856.

Protopanderodus cf. *P. varicostatus* (Sweet and Bergström)

Plate 3, figures 1-8,
Figure 3F

a/b-c element

?*Acontiodus robustus* (Hadding). NASEDKINA, 1975, Pl. 3, figs. 1, 2 [multicostate elements; = ?*P. varicostatus* (Sweet and Bergstrom) s.l., or ?*Scolopodus* sp.].

cf. *Scolopodus varicostatus* SWEET and BERGSTRÖM, 1962, p. 1247, 1248, Pl. 168, figs. 4-9, Fig. 1A, C, K.

Multielement

Protopanderodus cooperi (Sweet and Bergström). v BARNES and POPLAWSKI, 1973 (in part), p. 782, Pl. 4, fig. 8, unfigured hypotype GSC 30332 only [= quadricostate *a/b* elements; for other elements see *P. robustus* (Hadding), *P.* n. sp. A, herein]; ?LANDING, 1976 (in part), p. 638, 639, Pl. 4, fig. 6 only (= *a/b* element; may be part of *P. gradatus* Serpagli or *P. strigatus* Barnes and Poplawski; fig. 7 = *a/b* element of *P.* n. sp. A, herein).

Protopanderodus cf. *varicostatus* (Sweet and Bergström). LÖFGREN, 1978, p. 91, 92, Pl. 3, figs. 26-31 (includes synonymy); ZENG et al., 1983, Pl. 12, figs. 27-29; STOUGE, 1984, p. 51, 52, Pl. 3, figs. 11-17 (includes synonymy); ORCHARD in BERGSTRÖM and ORCHARD, 1985, Pl. 2.2, fig. 3.

Protopanderodus varicostatus (Sweet and Bergström). BERGSTROM, RIVA, and KAY, 1974, Pl. 1, figs. 9, 10; ?GASTIL and MILLER, 1981, Figs. 2j, k; TIPNIS, CHATTERTON, and LUDVIGSEN, 1978, Pl. 8, figs. 8, 12 (= *e*, *a/b-c* elements); ?SIMES, 1980, Fig. 6; AN et al., 1983, p. 132, Pl. 16, figs. 9-12 (= *a/b*, *c*, *e*, *e* elements, respectively); ?BURRETT, STAIT, and LAURIE, 1983, p. 184, Figs. C, D (= *a/b-c* element); vv NOWLAN and THURLOW, 1984, p. 293, 294, Pl. 2, figs. 1-3, 8 (= *e*, quadricostate *a/b-c*, gigantiform, tricostate *a/b* elements); AN et al., 1985, Pl. 12, figs. 1-4 (= *c*, *a/b*, *e*, *c* elements).

?*Protopanderodus varicostatus* (Sweet and Bergström)? vv NOWLAN, 1981a, p. 15, Pl. 1, fig. 5, Pl. 3, fig. 15 (= tricostate, sexicostate, i.e. four costae on one side and two on other side, *a/b* elements; poorly preserved, antero-aboral corners not complete).

Remarks. Two associations are distinguished: (1) *Protopanderodus varicostatus* (Sweet and Bergström) s.s. (Fig. 2) includes elements reported by Sweet and Bergström (1962), and Bergström (1978); and (2) *Protopanderodus* cf. *P. varicostatus* (herein) is based on the species of Löfgren (1978), and similar species of An et al. (1983, 1985), Bergström et al. (1974), Tipnis et al. (1978), Zeng et al. (1983), Nowlan and Thurlow (1984), Stouge (1984), Bergström and Orchard (1985), and northern Yukon (herein). The stratigraphic ranges of both forms overlap, as do the geographic ranges.

Protopanderodus cf. *P. varicostatus* differs from *P. varicostatus* s.s. by the following characteristics. The *a/b* elements have variably developed antero-aboral corners, which may be angular (Pl. 3, fig. 3, Fig. 3F), rounded (Pl. 3, figs. 1, 2, 6), or notched. The notch is not as deep as in the same elements of *P. varicostatus*. The *e* element is like *Scandodus unistriatus* Sweet and Bergström s.f., but the groove is more anterior (Löfgren, 1978, p. 91). The *e* element is only tentatively recognized in the limited northern Yukon material.

Most acontiodontiform elements of *Protopanderodus* cf. *P. varicostatus* sensu Löfgren (1978) have a total of three costae and thus are asymmetrical, whereas about 25 per cent of the elements of *Scolopodus varicostatus* s.f. reported by Sweet and Bergström (1962) are symmetrical (quadricostate); Löfgren (*ibid.*, p. 92) thought that the absence of symmetrical forms in her species was anomalous (see generic discussion, above). No truly symmetrical elements are present in the material from northern Yukon, although some quadricostate elements are subsymmetrical with respect to the position of the costae.

The only *e*? element is markedly asymmetrical in that it has a well developed costa posterior to a sharp edged groove on the inner face (Pl. 3, fig. 7). The outer face of this element has a prominent median costa and a planar face between this costa and the sharp anterior margin (Pl. 3, fig. 8). This *e*? element differs from the homologous element in *Protopanderodus* cf. *P. varicostatus* of Löfgren (1978), which lacks costae. It may alternatively be an unusual *a/b* element.

Stouge (1984) tentatively included *Acontiodus cooperi* Sweet and Bergström s.f. and comparable elements to represent the "missing" symmetrical element in his *Protopanderodus* cf. *P. varicostatus*. Dzik (1983, Fig. 3:29) illustrated a similar element within his *P. varicostatus*. Symmetrical bicostate elements such as these are regarded above as *c* elements of *P. robustus* (Hadding).

As in *Protopanderodus* cf. *P. varicostatus*, the *a/b-c* elements in *P.* cf. *P. varicostatus* sensu Stouge (1984) vary in base length and in development of the antero-aboral corner. This corner may be rounded or sinuous, forming an anterior notch that is not well developed. The *e* element of Stouge's species differs from the corresponding element in both *P. varicostatus* and *P.* cf. *varicostatus* sensu Löfgren in that the medial groove on the inner face is quite wide and shallow.

Stouge (1984) included the multicostate elements of *Protopanderodus rectus* (Lindström) sensu Dzik (1976) within his *P.* cf. *P. varicostatus*; this interpretation is followed herein.

The outer face of the slightly reclined, short-based gigantiform element (Pl. 3, figs. 4, 5) has a posterolateral costa, and the planar face between this costa and the sharp anterior margin is bisected by a narrow longitudinal groove. The inner lateral face has a median groove and an anterolateral costa on the cusp and thus differs from the gigantiform element of Nowlan and Thurlow (1984, Pl. 2, fig. 3). Their four gigantiform elements are similar to the homologous element (cf. herein, Pl. 3, fig. 16) of *P. liripipus* Kennedy et al. from northern Yukon, except that the outer face is acostate.

The *a/b* elements of *Protopanderodus* cf. *P. varicostatus* lack the flange-like keel on the posterior oral

margin of the base found in *P. insculptus* (Branson and Mehl) and the extended and tapered base found in *P. liripipus*.

Occurrences. Löfgren's (1978) species (shown as *P.* cf. *P. varicostatus* in Fig. 2) ranges from the upper *Paroistodus originalis* Zone to the *Pygodus serra* Zone (middle Arenig-Llanvirn) in Sweden. The figured specimens of Tipnis et al. (1978), shown as (*P. varicostatus*) in Figure 2, are from their section K of the Road River Formation in southwestern Northwest Territories and occur with *Amorphognathus variabilis* Sergeeva. Tipnis et al. assigned these strata to the upper Arenig – lower Llanvirn. Unfigured elements from their locality 5 are from upper Llanvirn strata (see *Protopanderodus liripipus* Kennedy et al., herein).

Protopanderodus varicostatus of Nowlan (1981a) and Burrett et al. (1983) are from the *Prioniodus* (*Baltoniodus*) *gerdae* Subzone of New Brunswick and southern Tasmania, respectively (see *P. varicostatus*? in Fig. 2).

Protopanderodus varicostatus sensu Gastil and Miller (1981; *P. varicostatus* s.l. in Fig. 2) from northwestern Mexico is significant because it occurs with species representing the *Oepikodus smithensis* Zone, thus being older than Löfgren's (1978) *P.* cf. *P. varicostatus*. One of their elements (*ibid.*, Fig. 2j) appears to have two costae on one face and is therefore a multicostate form. It is questionable whether this species represents *P.* cf. *P. varicostatus*, thereby lowering its first appearance, or *P. gradatus* Serpagli, which is found at the same stratigraphic interval.

Occurrences of other species in the synonymy are: (listed in alphabetical order of authors) An et al., 1985: Llanvirn, upper *E. pseudoplanus* to lowest *P. jianyeensis* (*E. suecicus* to *P. serra*) zones, Hubei Province, China; Bergström et al., 1974: *P. serra* to lower *P. anserinus* zones, north-central Newfoundland; Bergström and Orchard, 1985: *A. variabilis* to *E. suecicus* zones, southern Scotland; Nowlan and Thurlow, 1984: lower Whiterock (uppermost Arenig – lower Llanvirn), central Newfoundland (shown as (*P. varicostatus*) in Fig. 2); Simes, 1980: *P. anserinus*, and possibly, *P. serra* zones, New Zealand (*P. varicostatus*, Fig. 2); Stouge, 1984: *E. suecicus* Zone, western Newfoundland (shown as (*P.* cf. *P. varicostatus*) in Fig. 2); Zeng et al., 1983: *E. foliaceus* Zone, eastern Yangtze gorges, China.

Material. 13 *a/b*, 1 e, 1 gigantiform elements.

Figured specimens. GSC 82857-82862.

Protopanderodus n. sp. A

Plate 1, figures 11-24, 27, Plate 2, figures 1-9, Figure 3A-C

a? element

?*Scandodus dubius* BRADSHAW, 1969, p. 1161, Pl. 134, figs. 19-21; Fig. 4G, H.

a/b-c element

cf. *Acontiodus arcuatus* LINDSTRÖM, 1955, p. 547, 548, Pl. 2, figs. 2-4, Fig. 3A (may = c elements).

cf. *Acontiodus reclinatus* LINDSTRÖM, 1955, p. 548, 549, Pl. 2, figs. 5, 6, Fig. 3C (?*a/b* elements).

Acontiodus robustus (Hadding). BRADSHAW, 1969 (in part), p. 1148, Pl. 131, figs. 8, 10, 14 only [fig. 13 = ?gerontic *a/b* element of *P. robustus* (Hadding), herein]; v ?BARNES and POPLAWSKI, 1973 (in part), p. 768, 769, Pl. 2, fig. 15, unfigured hypotype GSC 30322 only (= c elements; other unfigured element is discussed below).

v *Acontiodus* sp. 3 UYENO and BARNES, 1970, p. 105, Pl. 21, figs. 10, 11, Fig. 7D (c element).

Scandodus pipa Lindström. v UYENO and BARNES, 1970, p. 115, 116, Pl. 22, figs. 6, 7, Fig. 7C (*a/b* element).

Scandodus cf. *S. pipa* Lindström. BRADSHAW, 1969, p. 1161, Pl. 135, figs. 3, 4 (*a/b* element).

e element

v ?*Acontiodus* sp. 1 UYENO and BARNES, 1970, p. 104, Pl. 21, figs. 1, 2, Fig. 7G.

?*Distacodus* sp. BRADSHAW, 1969, p. 1149, Pl. 131, figs. 3, 4.

?*Drepanodus* cf. *arcuatus* Pander. LINDSTRÖM, 1955, p. 560, 561, Pl. 2, figs. 45, 46, Fig. 4c.

Multielement

Drepanodus arcuatus Pander. LANDING, 1976, p. 632, Pl. 1, 5; figs. 16?, 17-19, 21-23 (= ?, *a*, *c*, *a*, *a/b*, *a/b*, *a/b* elements, respectively); cf. LÖFGREN, 1978 (in part), p. 51-53, Pl. 2, fig. 2 only (= *e* element).

(?)*Drepanodus arcuatus* Pander. ETHINGTON and CLARK, 1982 (in part), p. 36, 37, Pl. 3, fig. 6 only (= e element; figs. 4, 5, 12 = *D. arcuatus*).

?*Drepanoistodus* sp. B. TIPNIS, CHATTERTON, and LUDVIGSEN, 1978, Pl. 8, fig. 17 (= ?*a/b* element).

?*Protopanderodus arcuatus* (Lindström). TIPNIS, CHATTERTON, and LUDVIGSEN, 1978, Pl. 8, fig. 11 (= ?c element).

?*Protopanderodus* aff. *P. arcuatus* (Lindström). ETHINGTON and CLARK, 1982, p. 83, Pl. 9, fig. 10 (= ?c element).

Protopanderodus cooperi (Sweet and Bergström). v cf. BARNES and POPLAWSKI, 1973 (in part), p. 782, Pl. 3, fig. 1 only [= *a/b* element; for other elements, see *P. robustus* (Hadding), *P.* cf. *P. varicostatus* (Sweet and Bergström), and below]; LANDING, 1976 (in part), p. 638, 639, Pl. 4, fig. 7 only (= *a/b* element; fig. 6 = a? or *a/b* element, possibly of *P. gradatus* Serpagli, *P. strigatus* Barnes and Poplawski or *P. varicostatus*).

non *Protopanderodus reclinatus* (Lindström). v BARNES and POPLAWSKI, 1973, p. 782, 784, Pl. 3, figs. 2, 3, unfigured hypotypes GSC 30311-30314 (see below).

cf. *Protopanderodus* cf. *reclinatus* (Lindström). STOUGE, 1984, p. 51, Pl. 3, figs. 6-10 (= *a/b*, c, c, ?c, *a/b* elements, respectively).

?*Protopanderodus robustus* (Hadding). AN et al., 1983, p. 132, Pl. 15, fig. 21; STOUGE, 1984 (in part), p. 49, Pl. 2, figs. 3, 4 only (figs. 5-8 = *P. robustus*, herein); AN et al., 1985, Pl. 11, figs. 15, 16.

Remarks. Comments about synonymy. The synonymy is annotated to identify element morphotypes (e.g., *a* element) and to explain why some illustrated specimens of the listed form and multielement species are not part of *Protopanderodus* n. sp. A.

A further comment on some of the species listed in the synonymy is also necessary. *Drepanodus arcuatus* and *Protopanderodus arcuatus* are multielement species based on different form species. The former takes its name from *D. arcuatus* Pander s.f., the latter from *Acontiodus arcuatus* Lindström s.f. To add to the confusion, some writers consider *A. arcuatus* s.f. to be a junior subjective synonym of the multielement species *D. arcuatus*.

Drepanodus arcuatus is a valid multielement species. The multielement status of the type material of *Acontiodus arcuatus* Lindström s.f. is not known. It may be part of *Drepanodus arcuatus* Pander, or it (along with *Acontiodus reclinatus* Lindström s.f.) may be part of a species of *Protopanderodus* (see under Discussion of Trivial Name, below).

Comparison of elements. *Protopanderodus* n. sp. A includes acostate elements and a symmetry transition series of costate elements. The transition series is based on the costae number (one or two) and position (symmetrically or asymmetrically placed relative to the cusp and base). A single fused cluster of elements is used to show that the *c* and *e* elements are part of the same apparatus.

An *a* element cannot be proven to be part of this species' apparatus since it is not found in material from northern Yukon. However, a carinate element of *Drepanodus arcuatus* Pander illustrated by Landing (1976, Pl. 1, fig. 17) and one of *Protopanderodus* cf. *P. reclinatus* by Stouge (1984, Pl. 3, fig. 10) could be part of a similar species and may be interpreted as *a* elements. A less recurved element that is otherwise similar to these is *Scandodus dubius* Bradshaw s.f.

Scandodus dubius s.f. was tentatively included by Löfgren (1978) in her synonymy of *Protopanderodus robustus* (Hadding). Stouge (1984) placed this form species, plus *Scandodus biconvexus* Bradshaw s.f. and *Scandodus*? sp. Bradshaw s.f. in the multielement species *Scapellodus biconvexus*. The latter two form species are not considered to be related to *S. dubius* s.f. or *P.* n. sp. A.

The *a/b* element has sharp anterior and posterior cusp margins. It is similar in outline to *Scandodus pipa* Lindström s.f. but differs in that the outer cusp face has a posterior costa (Pl. 1, fig. 11; Fig. 3A). The inner face is carinate (Pl. 1, figs. 14, 18), as in *S. pipa* s.f. *Scandodus pipa* s.f. sensu Uyeno and Barnes and *S.* cf. *S. pipa* of Bradshaw (1969) are equated to the *a/b* element because there is a costa on the outer posterolateral margin, and the inner face is carinate.

In outline, *Acontiodus reclinatus* Lindström s.f. is like the *a/b* element of *Protopanderodus* n. sp. A. The ornamentation is also similar in the sense that "the posterior lateral costae are little accentuated, and sometimes absent" (Lindström, 1955, p. 549). One of the elements of *A. reclinatus* s.f. of Lindström (1955, Fig. 3C) is a *c* element in the sense that it has a symmetrical bicostate cross-section of the cusp. The base of this element is like that of the *a/b* element.

Drepanoistodus sp. B of Tipnis et al. (1978; shown herein as *D.* sp. B in Figure 2) has an inner face and outline that are similar to the *a/b* element of *Protopanderodus* n. sp. A, but no comment can be made concerning the ornamentation of the outer face because the type material is not readily available.

The *c* element (Pl. 1, figs. 12, 13, 19, 20, 24; Fig. 3B, C) is bicostate, strongly recurved, and the posterior margin of the cusp and proximal region of the base is sharp. It has a long base like *Acontiodus arcuatus* Lindström s.f. The cusp is more recurved and the costae are not as strong basally as in the *c* element of *Protopanderodus robustus*. The antero-aboral corner of the *c* element lacks the notch found on this element of *P. robustus*. The element of *P. robustus* illustrated by An et al. (1983) has a recurved cusp and weak costae similar to an element figured herein (Pl. 1, fig. 13) but differs in that the base is longer. The *c* element of *P. robustus* sensu Stouge (1984) is like the element figured by An et al. (1983). *Protopanderodus robustus* of An et al. (1983, 1985) also lack the antero-lateral notch and have basally weak costae.

Acontiodus robustus (Hadding) s.f. sensu Bradshaw (1969) and *Acontiodus* sp. 3 Uyeno and Barnes s.f. are similar to the *c* element in that they also have basally weak costae and are without an antero-aboral notch. *Acontiodus robustus* s.f. of Barnes and Poplawski (1973) differs in that it is quite sharply recurved. This form species of Barnes and Poplawski (1973) was assigned to *Protopanderodus robustus* by Löfgren (1978). Only the figured, and one of the unfigured hypotypes of *A. robustus* s.f. sensu Barnes and Poplawski (1973) are questionably assigned to *P.* n. sp. A.

The other unfigured hypotype (GSC 30321) of *Acontiodus robustus* s.f. of Barnes and Poplawski (1973) has a rather unusual base. This is posteriorly extended, subrectangular in lateral profile, and with nearly straight oral and aboral margins. The aboral margin curves upward to the posterior, and downward to the anterior, forming a slight antero-aboral notch. The cusp is recurved immediately above the low base. The posterior face of the cusp is flat and costate, and bound on each side by one costa, which does not extend to the aboral margin. The lateral faces of the cusp are planar to slightly concave. These faces and the sharp anterior edge give the cusp a triangular cross-section. The extended base and attitude of the aboral margin are like those of *Acontiodus rectus* var. *sulcatus* Lindström s.f. (1955, Pl. 2, fig. 13, only) and *Protopanderodus graeai* (Hamar) of Nowlan (1981a, Pl. 3, fig. 13, only). The cusp is more recurved than that in either species. Assignment of this particular element probably should be to *P. graeai* sensu Nowlan.

The *e* element (Pl. 1, figs. 15, 21-23; Pl. 2, fig. 2) corresponds closely to the *Drepanodus* cf. *D. arcuatus* s.f. discussed by Löfgren (1978) and Ethington and Clark (1982) and interpreted as being part of the multielement species, *D. arcuatus* and ?*D. arcuatus*, respectively. The latter authors (1982, p. 37) described their elements as having a blunt medial ridge on the outer face (in contrast to the rounded face of specimens of Lindström, 1955 and Löfgren, 1978), and the characteristic marked re-entrant in the basal margin of the outer face.

The *e* element has a short base that is strongly flexed to the inner side and has an anteriorly arched outer aboral margin. Its cusp has a costa on the posterior part of the outer face. The inner face of this element is unornamented. The same face of another element (Pl. 1, fig. 22) is carinate. *Distacodus* sp. s.f. of Bradshaw (1969) has this same arched margin but differs slightly in that both faces of the cusp are costate. The anterior edge of the base of *Distacodus* sp. s.f. is more keeled and flexed more inwardly than in the *e*

elements. *Acontiodus* sp. 1 s.f. of Uyeno and Barnes (1970) is comparable to *Distacodus* sp. s.f. The outer post-medial costa differs from the medial ridge found on the elements of Ethington and Clark (1982).

The fused cluster (Pl. 1, figs. 16, 17, 22, 23, 27) is composed of two *c* elements (best shown on the obverse side, Pl. 1, fig. 27) and one *e* element on the reverse side; the bases of both *c* elements and this *e* element are opposed. Fragments contained in this cluster include a short-based element (probably an *e* element – it has a shallow basal cavity but no aboral margin notch) and the cusps of two elements.

Relationship with *Drepanodus arcuatus* Pander

Elements of *Protopanderodus* n. sp. A are very similar to those of *Drepanodus arcuatus*. A conodont collection (GSC locality 99245) from the Swedish Lunne section (Segerstad Limestone) of Löfgren (1978) contains *D. arcuatus* (along with *P. parvibasis* Löfgren and *P.* cf. *P. varicostatus* (Sweet and Bergström) sensu Löfgren). The few pipaform elements appear to be acostate. The pipaform (*a/b*) element of *P.* n. sp. A is unicostate. Bicostate arcuatiform elements of *D. arcuatus* have very weak costae, although very large elements have stronger costae. Most of these elements are asymmetric due to the position or strength of the costae, or due to a lateral twisting of the cusp or antero-aboral keel. One graciliform(?) element has a short lateral costa. The bicostate *c* elements of *P.* n. sp. A have stronger costae and are not laterally twisted.

Elements of *Drepanodus* in the collection from Sweden are hyaline, and vary from being translucent in small, to opaque in large, elements. Most of the elements of *Protopanderodus* are albid with an indistinct boundary between white and hyaline matter. All elements of *P.* n. sp. A from northern Yukon are similarly albid, although the overall colour is darker. Unfortunately, white matter can be found in elements of *Drepanodus*, so this feature cannot be used to differentiate between the two genera.

The elements used in the reconstruction of *Drepanodus arcuatus* Pander by Landing (1976, p. 632) raises some questions concerning its generic affinity. The apparatus includes asymmetrically acostate to costate "*D. arcuatus*-type", symmetrically costate "*Acontiodus arcuatus*-type", and "pipaform" elements.

The majority of Landing's (1976) *Drepanodus arcuatus*-type elements are costate, and so are at least some of the pipaform (?asymmetrical acontiodontiform) elements. The ratios of costate *D. arcuatus* s.f. and acostate *A. arcuatus* Lindström s.f. computed by Fåhraeus and Nowlan (1978) from their material and data of others vary – 1:1, 3:1, 7:1. Elements of *D. arcuatus* sensu Löfgren (1978) presumably are mostly acostate, as Löfgren was unaware of any collection that had such a high percentage of costate elements as Landing's material. Löfgren (*ibid.*) suggested that the great relative abundance of costate elements of *D. arcuatus* sensu Landing (1976) may be an example of geographic variation within *D. arcuatus*.

The elements of *Drepanodus arcuatus* sensu Landing (1976), and of the similar northern Yukon *Protopanderodus* n. sp. A, show a costae-symmetry transition series and thus should be referred to *Protopanderodus* rather than *Drepanodus*.

The association of a scandodontiform (*e*) element and costate acontiodontiform (*a/b-c*) elements in a fused cluster from northern Yukon further supports assignment of these elements to *Protopanderodus* (Pl. 1, figs. 16, 17, 22, 23, 27; Pl. 2, figs. 1-5). As interpreted herein, *Drepanodus arcuatus*, sensu both Fåhraeus and Nowlan (1978) and Löfgren (1978), and the species of Landing (1976), are probably not conspecific. The generic assignment of *D. arcuatus* of the former two studies is still questionable. The apparatus, as reconstructed by these authors, is not dominated by costate elements and thus is more like *Drepanodus* than *Protopanderodus*. However, both reconstructions include *D.* cf. *D. arcuatus* s.f., a form that is similar to the *e* element of *P.* n. sp. A.

Although Ethington and Clark (1982) included elements like *Drepanodus* cf. *D. arcuatus* Pander sensu Lindström s.f. within their ?*D. arcuatus*, they noted differences in the stratigraphic occurrences of these elements. The few elements of the form species were not found below the middle of the Fillmore Formation (?upper Tremadoc-lower Arenig) in Utah, whereas the other elements of ?*D. arcuatus* had more extended upper and lower limits.

From a comparison of the elements from northern Yukon and those of Landing (1976), it is suggested that an acostate scandodontiform element questionably represents the *a* position in *Protopanderodus* n. sp. A. *Protopanderodus elongatus* Serpagli (1974, Fig. 16) and *P. gradatus* Serpagli (*ibid.*, Fig. 17) have some *a/b* elements that are unicostate and thus may be interpreted as *a* elements. Other species of *Protopanderodus* may also have an equivalent element masked in the subtle variations found in the acontiodontiform elements, or may simply be lacking an *a* morphotype.

Relationship with *Protopanderodus arcuatus* (Lindström)

Protopanderodus arcuatus (Lindström) sensu Tipnis et al. (1978) and *P.* aff. *P. arcuatus* of Ethington and Clark (1982) include the form species *Acontiodus arcuatus* Lindström s.f. Use of *A. arcuatus* s.f. as the senior subjective synonym is unfortunate, as elements of these multielement reconstructions can be quite similar to elements of the multielement species *Drepanodus arcuatus* Pander.

The illustrated elements of the species of both Tipnis et al. (1978) and Ethington and Clark (1982), are tentatively identified herein as *c* elements. Without illustration of the other elements of the apparatus, these species of *Protopanderodus* cannot be positively linked to *P.* n. sp. A. *Protopanderodus arcuatus* of An et al. (1985) s.f. and the form species *P. arcuatus* s.f. sensu Tipnis et al. (1978) are queried in Appendix and in Figure 2 because they are not illustrated and hence their relationships to *P.* n. sp. A are not known.

Relationship with *Protopanderodus reclinatus* (Lindström) s.l.

Stouge (1984) reconstructed the apparatus of *Protopanderodus* cf. *P. reclinatus* and included a number of junior synonyms, which are listed above under *P.* n. sp. A. Synonyms listed by Stouge for *P.* cf. *P. reclinatus* that are not included here are: *Oistodus* aff. *O. parallelus* Pander s.f. of Barnes and Poplawski (1973; illustrated elements are fragmentary) and *Panderodus* sp. Bradshaw s.f. This last form species has a faint outer costa on the oral surface of

the base; the inner face of the element lacks costae and instead appears to have a weak, broad groove (Stouge questionably included this form species in his reconstruction of *P.* cf. *P. reclinatus*).

Stouge (1984) illustrated two scandodontiform elements of *Protopanderodus* cf. *P. reclinatus*. One with a relatively low base (*ibid.*, Pl. 3, fig. 6) is similar to the *a/b* element herein, and another with a higher base (*ibid.*, Pl. 3, fig. 10) is like the element of Landing (1976, Pl. 1, fig. 17) that is suggested herein to be an *a* element.

Stouge (1984) included *Protopanderodus reclinatus* of Barnes and Poplawski (1973) under his *P.* cf. *P. reclinatus*. The type material of the species of Barnes and Poplawski has been viewed; the species is probably related to, but different from, that of Stouge (1984).

Five of the six hypotypes of *Protopanderodus reclinatus* sensu Barnes and Poplawski (hereafter *P. reclinatus*?) are pipaform. Unfigured hypotypes (GSC 30311, 30312, 30314) are quite similar to one of their illustrated (but lost) elements (*ibid.*, Pl. 3, fig. 2). These elements are strongly recurved and have a twisted cusp. The posterior margin is costate, and bound by a posterolateral costa on each face. The posterolateral costa on the inner face is weak and ends high on the base, whereas the strong costa on the outer face extends to the aboral margin, like that shown (*loc. cit.*). The anterior margin of the cusp is slightly keeled, but this does not extend onto the base. The antero-aboral margin is curved, not notched. The base of these elements is laterally compressed; the basal outline is relatively wide at the posterior, and narrows toward the anterior. The unfigured hypotype (GSC 30313) is also a pipaform element; it differs in that both posterolateral costae are subsymmetrically placed, and both costae end high on the more compressed base.

These elements, and an element of *P. cooperi* (Sweet and Bergström) illustrated by Barnes and Poplawski (1973, Pl. 3, fig. 1), have an outline like the *a/b* elements of *Protopanderodus* n. sp. A, and *Acontiodus reclinatus* s.f. The bicostate nature of these elements of *P. reclinatus*? is like that of *A. reclinatus* s.f. and differs from that of the *a/b* elements of *P.* n. sp. A and the element of *P. cooperi* mentioned above; both have a costa only on the outer face. These elements of *P. reclinatus*? are regarded as *a/b* elements, with possibly the subsymmetrical one being a *c* element. Although comparable to the *a/b* element of *P.* n. sp. A, the one element of *P. cooperi* sensu Barnes and Poplawski (1973) is probably associated with the bicostate forms.

The other figured element of *Protopanderodus reclinatus*? (Barnes and Poplawski, 1973, Pl. 3, fig. 3) has two primary costae that are subsymmetrically placed. The element has slight asymmetry in that the cusp and an antero-aboral keel are slightly deflected. Both lateral faces have secondary costae, although these are not visible in the illustration. The primary costa on the inner face bifurcates at the proximal part of the cusp; the outer face has two secondary costae that are parallel to the stronger one on the base and proximal part of the cusp. With respect to the primary costae, the secondary costae are located toward the anterior and posterior, on the inner and outer sides, respectively. The outline is like that of *Acontiodus arcuatus* s.f. as figured by Lindström (1955, Pl. 2, fig. 3); some elements of this form species have secondary costae. This element of *P. reclinatus*? differs from *A. arcuatus* s.f. in that the costae do not extend to the aboral margin. The element is thought to be a variety of *c* element because of its secondary ornamentation.

An *e* element for the reconstructed apparatus of *Protopanderodus reclinatus*? may be found in *P. cooperi* of Barnes and Poplawski (1973, Pl. 3, figs. 4, 5, unfigured hypotypes GSC 30317-30319). These elements have a twisted base and smooth outer face on the cusp. One element (*ibid.*, Pl. 3, fig. 4) has a weakly costate inner face; the inner face on the other elements appear to be acostate.

Protopanderodus reclinatus? differs from *P.* n. sp. A in that its *c* element has a very short base with a straight rather than convex aboral margin. Also, the *e* element lacks a costa on the outer lateral face.

To summarize, *Protopanderodus reclinatus*? comprises all elements of *P. reclinatus* sensu Barnes and Poplawski (1973, Pl. 3, fig. 2, unfigured hypotypes GSC 30311, 30312, 30314 = markedly asymmetrical *a/b* elements; Pl. 3, fig. 3, unfigured hypotype GSC 30313 = subsymmetrical *c* elements), and possibly *e* elements that were originally assigned by Barnes and Poplawski (1973) to *P. cooperi* (*ibid.*, Pl. 3, figs. 4, 5, unfigured hypotypes GSC 30317-19). *Protopanderodus reclinatus*? is not conspecific with *P.* cf. *P. reclinatus* sensu Stouge, which is more closely related to *P.* n. sp. A.

The upper Arenig to lower Llanvirn *Protopanderodus* cf. *P. reclinatus* may be an ancestor of *P.* n. sp. A. The latter species occurs in the younger *Pygodus serra* Zone of northern Yukon; this same zone yielded unfigured elements assigned to *P. arcuatus* s.f. by Tipnis et al. (1978, Table IV). These writers also figured the multielement species, *P. arcuatus*, from the upper Arenig to lower Llanvirn. A link between these three species from northwestern Canada is somewhat circumstantial, but it is preferable to illustrate this lineage rather than a direct one involving *P.* cf. *P. reclinatus*. The speculative relationship between these species and *P.* cf. *P. reclinatus* is illustrated as iterative evolution (Fig. 2).

Discussion of trivial name

The multielement affinity of the type material *Acontiodus reclinatus* s.f. is not known. It may be part of *Drepanodus arcuatus*, *Protopanderodus reclinatus*? (as used herein) or *P.* n. sp. A. The holotype is from the middle Arenig *Oepikodus smithensis* Zone of Sweden (Lindström, 1955). *Scandodus pipa* s.f., *Drepanodus arcuatus* s.f., *D.* cf. *D. arcuatus* s.f. and *D. sculponea* Lindström s.f. are from the same strata of Sweden and were included within the multielement species *D. arcuatus* by Serpagli (1974), Löfgren (1978), and others. Löfgren also included *Acontiodus arcuatus* s.f., which is also present in Lindström's strata, in *D. arcuatus*.

Because of the similarities between elements of *Drepanodus arcuatus* and *Protopanderodus* n. sp. A, it is difficult to assign the above mentioned form species of Lindström (1955) to one or the other genus (see also generic discussion). The distribution of these six form species in Lindström's sections may provide evidence for generic assignment – they occur in the Lower and Upper Planilimbata Limestone. However, there are some differences in the occurrences (Lindström, 1955, Pl. 8-10; comments made below follow the erratum to the tables noted in Lindström, 1957, p. 166 – figures are moved two columns to the right relative to the headings).

Drepanodus arcuatus s.f. and *Scandodus pipa* s.f. are more common in the Lower Planilimbata Limestone and

underlying *Ceratopyge* beds. These strata represent the *Paltodus deltifer* and *Paroistodus proteus* zones. *Drepanodus* cf. *D. arcuatus* s.f. and *D. sculponea* s.f. are found throughout the Planilimbata Limestone. *Acontiodus arcuatus* s.f. and *A. reclinatus* s.f. (Lindström, 1955, Pl. 10) occur in strata of the Upper Planilimbata Limestone; only at Yxhult, Section II (samples 4 and 5) does *A. reclinatus* s.f. occur in the Lower Planilimbata Limestone. Although the distribution and relative abundance of the elements suggest a *D. arcuatus* association in the lower part of Lindstrom's section, and an *A. arcuatus* s.f.-*A. reclinatus* s.f. association in the younger parts, the evidence is simply too tenuous to make a formal statement in the above synonymy.

Scandodus dubius s.f. is not used as the senior synonym since 1) an element of this form is not recognized in material from northern Yukon; 2) it is not as recurved as the *a*? element in Landing (1976); and 3) it may alternatively be part of *Protopanderodus robustus* as suggested by Lofgren (1978). The present species is regarded as a new species of *Protopanderodus* because of the morphological and stratigraphic differences; it has the most similarities with *P.* cf. *P. reclinatus* sensu Stouge (1984).

Occurrences. *Protopanderodus* cf. *P. reclinatus* of Stouge (1984) occurs sporadically from the middle *Amorphognathus variabilis-Microzarkodina ozarkodella* Subzone and is more abundant throughout the *Eoplacognathus suecicus – Panderodus sulcatus* Subzone of western Newfoundland (Fig. 2); *P. robustus* of Stouge occurs in this latter zone.

Species of Tipnis et al. (1978) occur with *A. variabilis* Sergeeva and are upper Arenig to lower Llanvirn (their Section K; *P. arcuatus* in Figure 2, herein); unfigured elements of *P.* cf. *P. arcuatus* s.f. from lower strata of Section K of Tipnis et al. occur with *Oepikodus smithensis* Lindstrom; *Drepanodus* cf. *D. arcuatus* and unfigured elements of *P. arcuatus* s.f. (both queried in Figure 2) are listed from their locality 5 (middle – upper Llanvirn) in southwestern Northwest Territories.

The species of *Protopanderodus* that is shown in Figure 2 as ?*P. arcuatus* is from the Hubei Province of China. An et al. (1985) do not illustrate this species, but in a distribution table (*ibid.*, Fig. 3), it is shown to occur with *Oepikodus smithensis*, *Prioniodus* (*Baltoniodus*) *navis* Lindström, *Paroistodus originalis* (Sergeeva), *Protopanderodus gradatus* Serpagli and *Drepanodus arcuatus* Pander (among other species). Their illustrated *D. arcuatus* elements (*ibid.*, Pl. 4, figs. 6-11, Pl. 8, fig. 22, Pl. 12, figs. 10-13, 15) lack costae so it is reasonable to concur with the generic designation; however, it is interesting that they show the upper limit of the range of *D. arcuatus* as being within the *Hamarodus europeaus* Zone (upper *Amorphognathus tvaerensis* to lower *A. superbus* zones; upper Caradoc).

Occurrences of other species in the synonymy are (listed in alphabetical order of authors): An et al., 1983, north China; Barnes and Poplawski, 1973, uppermost Arenig to lower Llanvirn, southwestern Quebec (*P. reclinatus*? in Fig. 2); Bradshaw, 1969, Middle Ordovician (uppermost Arenig to lower Llanvirn), western Texas; Ethington and Clark, 1982, *O. communis* – "*M*". *marathonensis* to *J. gananda–R. andinus* intervals (*O. smithensis* Zone), Ibex area, Utah (*P.* aff. *P. arcuatus* in Fig. 2); Landing, 1976, *O. smithensis* Zone, eastern New York (shown as (*D. arcuatus*) in Fig. 2); Uyeno and Barnes, 1970, upper Arenig to lower Llanvirn, southwestern Quebec.

Material. 4 *a/b*, 7 *c*, 1 *e* elements, 1 fused cluster.

Figured specimens. GSC 82863-82872.

Protopanderodus sp. B

Plate 2, figures 26, 27

a/b-c element

?*Scolopodus*? *insculptus* (Branson and Mehl). SERPAGLI, 1967 (in part), p. 97, 98, Pl. 28, figs. 5a-6b only (other elements are equated herein with *P. insculptus* and *P. liripipus* Kennedy et al.).

Multielement

non *Protopanderodus gradatus* SERPAGLI, 1974, p. 75-77, Pl. 15, figs. 5a-8b, Pl. 26, figs. 11-15, Pl. 30, figs. 1a, b, Fig. 17; LANDING, 1976, p. 639, Pl. 4, figs. 8, 9, 11, 12; HIGGINS in BERGSTRÖM and ORCHARD, 1985, Pl. 2.1, figs. 16, 18; DUAN, 1985, Pl. 2, figs. 44, 45.

non *Protopanderodus strigatus* BARNES and POPLAWSKI, 1973, p. 784, Pl. 3, figs. 14, 17, Fig. 7E (types viewed; = *a/b* elements); STOUGE, 1984, p. 50, Pl. 2, figs. 15, 16, 18-24.

Remarks. The single *a/b* element (Pl. 2, fig. 27) of *Protopanderodus* sp. B is multicostate like homologous elements of *P.* cf. *P. varicostatus* (Branson and Mehl) and *P. insculptus* (Sweet and Bergström), both of which are identified in the same sample from northern Yukon, and *P. gradatus* Serpagli and *P. strigatus* Barnes and Poplawski. The short bases and lack of an antero-aboral notch are characteristic of both *P. gradatus* and *P. strigatus*. *Protopanderodus strigatus* differs from elements of *P. gradatus* and *P.* sp. B in that the *a/b* elements have a very noticable groove on one side, and commonly a weaker groove on the other. The element of *P. gradatus* illustrated in Bergström and Orchard (1985) is symmetrical and has a groove on both sides of the posterior margin.

The *c* element (Pl. 2, fig. 26) has costae that do not extend to the basal margin. This character is found in elements of *Protopanderodus* sp. Löfgren; the *c* element from northern Yukon is especially similar to one of the elements of *P.* sp. Löfgren (cf. Löfgren, 1978, Pl. 3, fig. 9). Löfgren (1978) identified 60 specimens of her species but made no mention of their having more or less than two costae. The base lacks the antero-aboral notch as found on the *c* element of *Protopanderodus robustus* (Hadding).

Protopanderodus gradatus and *P. strigatus* are similar to *P.* sp. B in that they include short-based elements with one costae on each lateral face, like the *c* element herein. Kennedy et al. (1979) noted two similar elements within *Scolopodus*? *insculptus* (Branson and Mehl) s.f. of Serpagli (1967). They included the remaining elements of Serpagli (1967) within *P. liripipus* Kennedy et al. because the elements have a total of three or more lateral costae. The two elements from Serpagli (1967) that are tentatively assigned to *P.* sp. B differ from its *c* element in that the costae are more medial, and the posterior part of the base is more aborally extended.

Occurrences. *Protopanderodus* sp. B occurs with *P. robustus* (Hadding), *P.* cf. *P. varicostatus*, *Periodon aculeatus* Hadding and *Walliserodus ethingtoni* (Fåhraeus), and based on the range of the last species, could range anywhere from *Amorphognathus variabilis – Microzarkodina ozarkodella* Subzone to *Pygodus anserinus* Zone (lower Llanvirn – upper Llandeilo).

The type material of *Protopanderodus gradatus* is from the *Oepikodus smithensis* and possibly the *Prioniodus (Baltoniodus) navis* zones of west-central Argentina (Serpagli, 1974). Landing (1976) identified *P. gradatus* from eastern New York and assigned it to the *O. smithensis* Zone. *Protopanderodus gradatus* is also reported from middle or upper Canadian to lower Whiterockian strata of northern Scotland (Bergström and Orchard, 1985) and uppermost Canadian strata of Arkansas (Ethington and Repetski, 1986).

Protopanderodus strigatus was originally described from the lower Llanvirn of southwestern Quebec by Barnes and Poplawski (1973). *Protopanderodus strigatus* sensu Stouge (1984) occurs in the lower *Amorphognathus variabilis – Microzarkodina ozarkodella* to upper *Eoplacognathus suecicus – Panderodus sulcatus* subzones of western Newfoundland. Because of the limited data, no further comment can be made concerning the affinity of *P.* sp. B.

Material. 1 *a/b*, 1 *c* elements.

Figured specimen. GSC 82873, 82874.

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APPENDIX

Stratigraphic ranges of *Protopanderodus* and *Drepanodus* species shown in Figure 2. Some species are junior synonyms; see text for details. Ranges below in parentheses are the interpretations of this author. Zonal schemes used in Figure 2 and below are primarily from Bergström (1971, 1983), Ethington and Clark (1971, 1982), Lindström (1971) and Löfgren (1978).

D. arcuatus: late Tremadoc *P. deltifer* Zone (Lindström, 1971) to at least *E. foliaceus* Subzone (Löfgren, 1978)

(*D. arcuatus*): *O. smithensis* Zone (Landing, 1976)

?*D.* cf. *D. arcuatus*: *P. serra* Zone (Tipnis et al., 1978)

D. sp. B: upper Arenig to lower Llanvirn (*D.* sp. B = *Drepanoistodus* sp. B), Tipnis et al. (1978)

P. arcuatus: upper Arenig to lower Llanvirn (Tipnis et al., 1978)

?*P. arcuatus*: (?*O. smithensis* to ?*P. originalis* zones), An et al. (1985)

?*P. arcuatus* s.f.: *P. serra* Zone (Tipnis et al., 1978)

P. aff. *P. arcuatus*: *O. communis* – "*M*". *marathonensis* to *J. gananda* – *R. andinus* intervals (*O. smithensis* Zone), Ethington and Clark (1982)

P. elongatus s.s.: Assemblage Zones B, C (*O. smithensis* to ?*P.* (*B.*) *navis* zones), Serpagli (1974)

P. elongatus: *J. gananda–R. andinus* interval (*O. smithensis* to ?*P.* (*B.*) *navis* zones), Ethington and Clark (1982)

(*P. elongatus*): Fauna D (*P. deltifer* to *P. proteus* zones), Repetski (1982)

P. gradatus s.s.: Assemblage Zones B, C (*O. smithensis* to ?*P.* (*B.*) *navis* zones), Serpagli (1974)

P. gradatus s.l. (comprises *P. gradatus*, *P.* cf. *P. gradatus* sensu Repetski): Fauna 1 (middle *O. smithensis* to *P.* (*B.*) *triangularis* zones), Repetski (1982)

P. gradatus: *O. communis* – "*M*". *marathonensis* to *P. costatus* – *C. rigbyi* – *H. holodentata* intervals (*O. smithensis* to *A. variabilis* zones), Ethington and Clark (1982)

P. graeai: upper *A. variabilis-M. ozarkodella* Subzone to *P. serra* Zone (Löfgren, 1978)

(*P. graeai*): *P. anserinus* Zone (Hamar, 1966), *P.* (*B.*) *variabilis* Subzone (Nowlan, 1981a)

P. insculptus: ?*P. insculptus* Zone (Ashgill; upper *A. superbus* to *A. ordovicicus* zones), Zeng et al. (1983)

P. cf. *P. insculptus*: *P. serra* Zone (Tipnis et al., 1978)

P.? *leei*: Fauna D (*P. deltifer* to *P. proteus* zones), may be species of *Semiacontiodus* (see text), Repetski (1982)

P. leonardii s.s.: Assemblage Zones A-C (*P.* (*P.*) *elegans* to ?*P.* (*B.*) *navis* zones), Serpagli (1974)

P. leonardii: *J. gananda-R. andinus* to *P. cryptodens-H. altifrons-M. auritus* intervals (*O. smithensis* to *P.* (*B.*) *navis* zones), Ethington and Clark (1982)

(*P. leonardii*): upper Fauna D-lower Fauna 1 (upper *P. proteus* to middle *O. smithensis* zones), Repetski (1982)

P. liripipus: *P. gerdae* Subzone (Kennedy et al., 1979) to *A. ordovicicus* Zone (Zeng et al., 1983; An et al., 1985)

P. cf. *P. liripipus*: middle *A. variabilis-M. ozarkodella* to upper *E. suecicus-P. sulcatus* subzones (Stouge, 1984)

P. parvibasis s.s.: middle *A. variabilis-M. ozarkodella* to lower *E. suecicus-P. sulcatus* subzones, Löfgren (1978)

P. parvibasis: *P. serra* Zone (herein)

P. reclinatus?: lower Llanvirn (uppermost Arenig to lower Llanvirn), Barnes and Poplawski (1973)

P. cf. *P. reclinatus*: middle *A. variabilis-M. ozarkodella* to upper *E. suecicus-P. sulcatus* subzones (Stouge, 1984)

P. rectus: lower *O. smithensis* Zone to lower *A. variabilis-M. ozarkodella* Subzone (Löfgren, 1978)

P. rectus?: *P. variabilis* Subzone (Nowlan, 1981a)

P. cf. *P. rectus*: uppermost Fauna D-lower Fauna 1 (upper *P. proteus* to middle *O. smithensis* zones), Repetski (1982)

P. robustus: uppermost Arenig to early Llanvirn (Nowlan and Thurlow, 1984), lower *E. suecicus-S. gracilis* Subzone to Caradoc (Löfgren, 1978), *P. gerdae* Subzone (Burrett et al., 1983)

P. strigatus: lower *A. variabilis-M. ozarkodella* to upper *E. suecicus-P. sulcatus* subzones (Stouge, 1984)

P. varicostatus s.s.: *P. anserinus* Zone (Sweet and Bergström, 1962; Bergström, 1978)

P. varicostatus s.l.: *O. smithensis* Zone (Gastil and Miller, 1981)

P. varicostatus: *P. anserinus* Zone (Simes, 1980)

(*P. varicostatus*): uppermost Arenig to lower Llanvirn (Tipnis et al., 1978; Nowlan and Thurlow, 1984)

P. varicostatus?: *P.* (*B.*) *gerdae* Subzone (Nowlan, 1981a; Burrett et al., 1983)

P. cf. *P. varicostatus*: upper *P. originalis* to *P. serra* zones (Löfgren, 1978)

(*P.* cf. *P. varicostatus*): *E. suecicus* Zone (Stouge, 1984)

P. cf. *P. varicostatus*: *P. serra* Zone (herein)

P. sp. Dzik (1983): upper Oil Creek Formation, Oklahoma (*P. originalis* to *E. suecicus* zones), Sweet and Bergström (1976)

P. sp. Löfgren: upper *P. originalis* to lower *M. f. parva* zones (Löfgren, 1978)

P. n. sp. A: *P. serra* Zone (herein)

P. sp. B: *A. variabilis-M. ozarkodella* Subzone to *P. anserinus* Zone (herein)

PLATE 1

All are lateral views, except where noted;
all are from PR:358.1-362.7 m

Figures 1-10. *Protopanderodus robustus* (Hadding)

1, 6. *c* elements: GSC 82850, short-based element, x54; GSC 82853, long-based element, x56.
2, 4. *a/b* element: GSC 82851, outer and inner lateral views, x55, x58.
3, 5. *e* element: GSC 82852, outer and inner lateral views, x74, x80.
7, 8. *e* element: GSC 82854, outer and inner lateral views, x93.
9, 10. *e* elements: GSC 82855, x122; GSC 82856, x73.

Figures 11-24, 27. *Prot anderodus* n. sp. A

11. *a/b* element: GSC 82863, costate face, outer lateral view, x59.
14, 18. *a/b* elements: acostate face, inner lateral view; GSC 82866, x68; GSC 82869, x43. (See also Pl. 2, figs. 6, 7).
12. *c* element: GSC 82864, x57.
13. *c* element: GSC 82865, x70.
19. *c* element: GSC 82870, x54.
20. *c* element: GSC 82871, x55.
24. *c* element: GSC 82872, x78.
15, 21. *e* element: GSC 82867, outer and inner lateral views, x79. (See also Pl. 2, figs. 8, 9).
16, 17, 27. fused cluster: GSC 82868, obverse side, x39, x48, x48. (See also Pl. 2, figs. 1-5).
22, 23. fused cluster: GSC 82868, reverse side (showing *e* element), x108, x39.

Figures 25, 26, 28, 29. *Protopanderodus parvibasis* Löfgren

25, 26. *c* elements: GSC 82847, x81; GSC 82848, x80.
28, 29. *e* element: GSC 82849, outer and inner lateral views, x82, x78.

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PLATE 2

All are lateral views, except where noted. All are from PR:358.2-362.7 m. Left figures of stereopairs are at 5° tilt; right figures are at 10° tilt

Figures 1-9. *Protopanderodus* sp. A

1-5. Fused cluster of elements: GSC 82868. (See also Pl. 1, figs. 16, 17, 22, 23, 27).
   1. Stereopair, reverse side (arrow indicates *e* element), x64.
   2. *e* element visible in Pl. 2, fig. 1, x135.
   3. Detail of fused cusp of *a/b*-*c* element on obverse side of fused cluster shown by arrow in Pl. 2, fig. 4, x192.
   4. Stereopair, obverse side (arrow indicates cusp shown in Pl. 2, fig. 3), x64.
   5. Oblique view, obverse side, x48.

6. *a/b* element: GSC 82869, stereopair, costate face, outer view, x66 (also shown in Pl. 1, fig. 18).
7. *a/b* element: GSC 82869, acostate face, inner view, x66.
8. *e* element: GSC 82867, stereopair, outer view, x138 (also shown in Pl. 1, figs. 15, 21).
9. *e* element: GSC 82867, stereopair, inner view, x138.

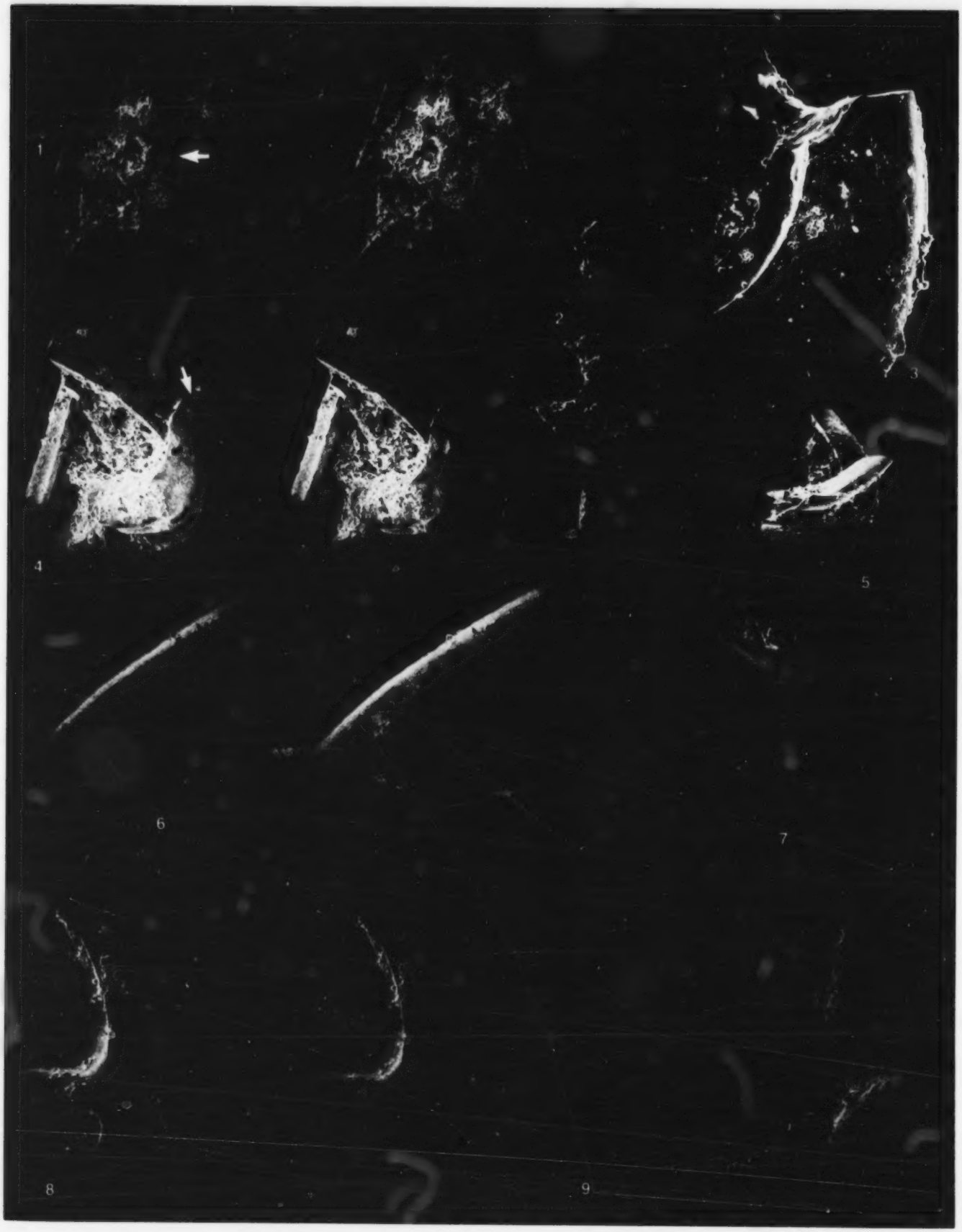
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PLATE 3

All are lateral views and are from PR:452.6 m, except where noted

Figures 1-8. *Protopanderodus* cf. *P. varicostatus* (Sweet and Bergström)

1. *a/b* element: GSC 82857, x61.
2. *a/b* element: GSC 82858, x58.
3. *a/b* element: GSC 82859, x55.
6. *a/b* element: GSC 82861, x58.

4, 5. gigantiform element: GSC 82860, inner and outer lateral views, x63, x60.

7, 8. *e*? element: GSC 82862, inner and outer lateral views, x56, x60.

All are from PR:358.1-362.7 m.

Figures 9-14, 17, 19. *Protopanderodus insculptus* (Branson and Mehl)

9. *a/b* element: GSC 82829, x120.
10. *a/b* element: GSC 82830, x58.
12. *a/b* element: GSC 82832, x56.
17. *a/b* element: GSC 82835, x60.
11. *c* element: GSC 82831, x147.
14. gigantiform element: GSC 82834, x57.

13, 19. *e* elements: GSC 82833 (specimen lost); GSC 82836, x55.

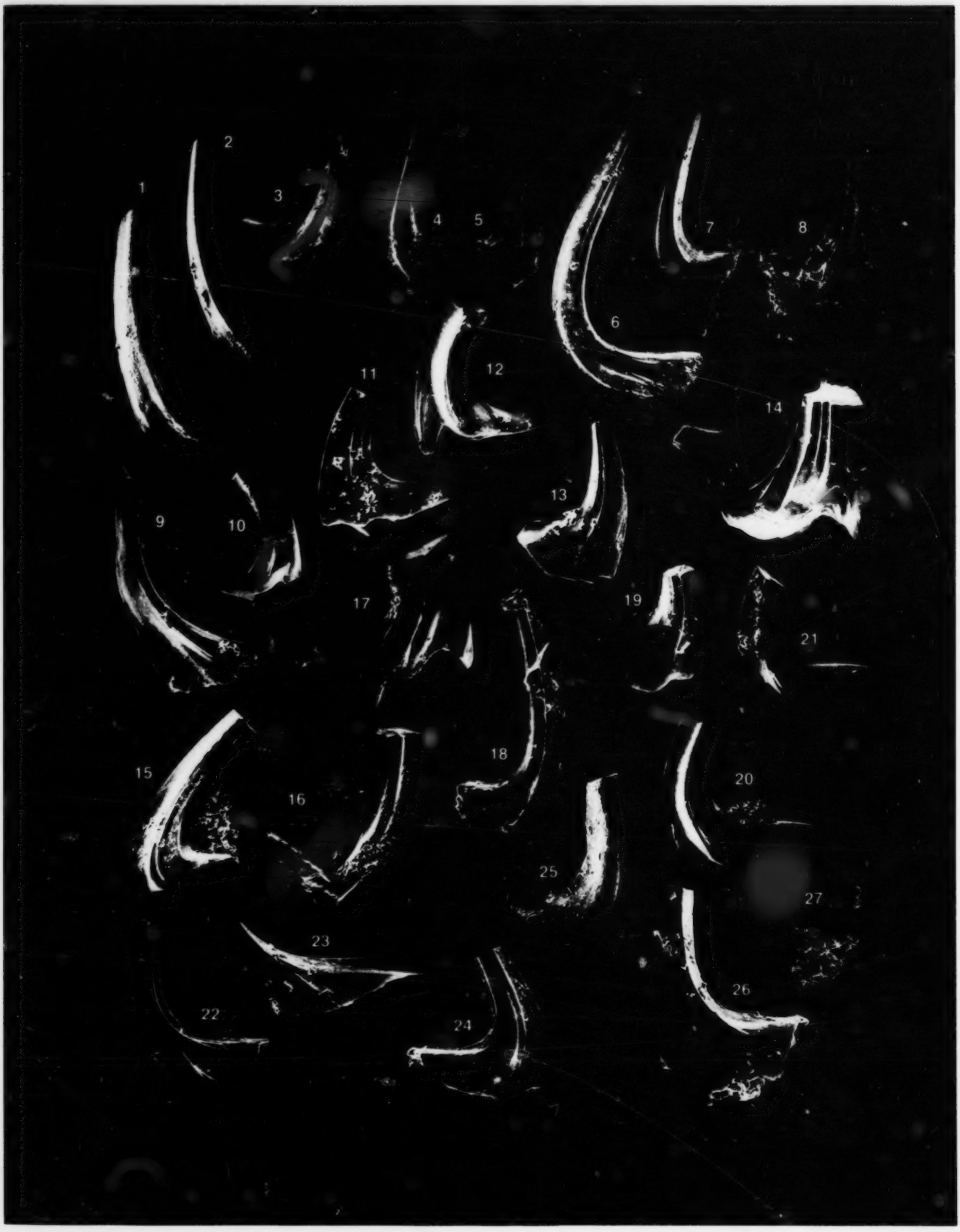
Figures 15, 16, 18, 20-25. *Protopanderodus liripipus* Kennedy, Barnes, and Uyeno

15. *a/b* element: GSC 82838, x61.
18. *a/b* element: GSC 82840, x126.
24. *a/b* element: GSC 82845, x100.
16. gigantiform element: GSC 82839, x55.
20. *c* element: GSC 82841, x50.
21. *c* element: GSC 82842, x67.
22. *c* element: GSC 82843, x140.
23. *c* element: GSC 82844, x105.
25. *c* element: GSC 82846, x66 (BR:50.3 m).

Figures 26, 27. *Protopanderodus* sp. B

26. *c* element: GSC 82873, x164.
27. *a/b* element: GSC 82874, x23.

Both are from TC:39 m.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